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Sexual Selection in the Ring-tailed Lemur (*Lemur catta*): Female Choice, Male Mating Strategies, and Male Mating Success in a Female Dominant Primate

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by

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Dedication

To my grandfather, Santiago Parga

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Sexual Selection in the Ring-tailed Lemur (*Lemur catta*): Female Choice, Male Mating Strategies, and Male Mating Success in a Female Dominant Primate

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Where male-male mating competition is intense, males are frequently larger than females, or have weaponry (e.g. enlarged canines) that females lack. Male dominance over females is often thought to be a by-product of selection for superior size and aggression. Paradoxically, some Malagasy primates show aggressive male-male competition over access to mates, yet lack sexual dimorphism in body size and dentition, and exhibit female dominance over males. This study's purpose was to investigate female choice and male mating strategies in one such species, the ring-tailed lemur (*Lemur catta*), to compare the success of physically combative male mating strategies versus alternative non-combative strategies (i.e. sneak copulations). Data were collected across five breeding seasons (2000-2004) on St. Catherines Island, USA, on a provisioned free-ranging *L. catta* population. Four distinct *L. catta* groups were studied, two per breeding season, each group having 4-8 females and 2-4 non-natal males. The most commonly used male mating tactics were those that depended on physical contest

competition among males. Alpha males often used their dominance status to gain first access to an estrus female, while non-alpha males frequently employed the use of dominance rank reversals as a mating strategy, which required aggressive challenges of more dominant males. Sneak and evasive copulations were also used, though much less often. Male sexual coercion of a female was also documented for the first time in this species. Male inter-troop transfer may be considered a successful mating strategy as well, for females in this study showed greater sexual preference for novel males, and males had higher mating success following a transfer. Female multiple mating was found to be extremely common. Although females mated with multiple males, alpha males were more likely to ejaculate earlier with a female than subordinate males, which may result in alpha males having higher reproductive success. In conclusion, physically combative competition appears to be critical to male mating success in *L. catta*. These findings provide further support for the hypothesis that sexual monomorphism in this species may have evolved because sperm competition or male stamina is more important than large body size in determining male reproductive success.

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CHAPTER 1: INTRODUCTION

Sexual Selection

The theory sexual selection first originated with Darwin (1859, 1871), who identified its two components, *intra-sexual selection*, which occurs when members of one sex (most often males) compete for mates, and *inter-sexual selection* (also known as epigamic selection or mate choice), which occurs when the activities of one sex affect the differential reproductive success of members of the opposite sex (Huxley, 1938). Darwin (1871) regarded male-male mating competition among animals as far more intense than female-female competition for mates, and observed that females appeared to be doing the 'choosing' with respect to mating partners. However, the limiting factors for male and female reproductive success were not identified until Bateman (1948) conducted laboratory experiments on fruit flies (*Drosophila melanogaster*), which established that male reproductive success is more variable than among females, and can far exceed female reproductive success. Bateman (1948) also established that the number of females inseminated is the primary limiting factor for male reproductive success. These findings, coupled with Williams' (1966) and Trivers' (1972) contributions showing that females of many species invest more reproductive effort and parental investment in offspring than males provided the framework for modern sexual selection theory.

Modern studies of sexual selection are largely experimental, and often involve research on taxa with short generation times (i.e. invertebrates: Clark et al., 1999) and/or social and sexual behavior that is minimally disrupted by researcher manipulation (e.g.

fish: Kingston et al., 2003). Taxa exhibiting these characteristics allow researchers to effectively isolate different variables thought to be important in inter-sexual mate choice decisions or intra-sexual competition over mates. An emphasis has also traditionally been placed on investigating how an animal's physical appearance determines its attractiveness to members of the opposite sex. For example, to test female mate choice preferences, researchers have altered male phenotypic characteristics experimentally by changing an individual's body coloration or other aspect of physical appearance, then recording female social or sexual preferences (e.g. Andersson, 1982; Burley, 1988; Burley and Symanski, 1998).

Primatology, in contrast, has historically focused less on the importance of physical appearance to mate choice decisions, and has placed a stronger emphasis on social traits, such as an individual's dominance status (Altmann, 1962) or affiliative behavior with others (Strum, 1982, 1994). The main reason for this focus on male social rather than physical traits is that many primate females co-exist in a much more permanent association with males (Smuts et al., 1987; Campbell et al., 2007) than do females of many other animal species, which allows primate females to assess male quality and/or the benefits to be gained by association with males over a longer period of time than is possible in species where males and females spend less time together or only come together to mate. It might therefore be expected that female primates would use male social traits more extensively than physical traits in mate selection (Setchell and Kappeler, 2003).

Another frequent difference between studies of sexual selection in primates versus those on other animal taxa is in research methodology. Experimental approaches commonly used for other animal species are often extremely difficult or impossible to carry out with non-human primates (Maestripieri and Kappeler, 2002), both because of the ethical issues surrounding non-human primate research in captivity and because studying non-human primates in their natural habitats entails many logistical challenges (Setchell and Curtis, 2003). Non-human primates are long-lived, have long generation times, are highly intelligent, and are socially complex (Dunbar, 1988). All of these traits complicate research methodology, increase the amount of time required to complete studies, and broaden the likelihood of confounding variables affecting the interpretation of results. Nevertheless, sexual selection research involving non-human primates has undergone dramatic advances in the last few decades, resulting in a much more complete view of female mate choice and male-male competition in this taxonomic group (Dixson, 1998; Paul, 2002; Jones, 2003; Setchell and Kappeler, 2003; Kappeler and van Schaik, 2004; Campbell, 2007; Manson, 2007).

Female Mate Choice

Among non-human primates, females are almost always the focus of mate choice studies because their greater parental investment (Trivers, 1972) is expected to make them sexually "choosier" than males (Small, 1989). When choosing among potential mates, there are several factors which can potentially be important in a female's decision, but all potential reasons can be classified into two general categories. First, females may

select mates based upon direct benefits they or their offspring might receive. Such direct benefits from males can include food (Tutin, 1979), protection from infanticide (Palombit et al., 1997), or parental care (van Schaik and Paul, 1996). Secondly, some females may select for mates based upon the genetic benefits their offspring could receive from such males (Orians, 1969).

Potential genetic benefits females can receive from males may take many forms. Traditionally, it has been thought that females often select for heritable genetic quality, or "good genes" (Andersson, 1994). Because high dominance status is commonly thought to signal genetic quality and superior fitness among animals (Cox and Le Boeuf, 1977), it might be expected that all females will select for the most dominant males. Indeed, female mate choice for dominant males has been found in several species of primate (baboons, *Papio cynocephalus*: Seyfarth, 1978; capuchins, *Cebus apella*: Janson, 1984; Welker et al., 1990; Phillips et al., 1994; Linn et al., 1995; Lynch, 2001; chimpanzees, *Pan troglodytes*: Matsumoto-Oda, 1999; howler monkeys, *Alouatta palliata*: Jones, 1985; golden lion tamarins, *Leontopithecus rosalia*: Baker et al., 1993; vervets, *Cercopithecus aethiops*: Keddy, 1986; sifaka, *Propithecus verreauxi*: Brockman, 1999).

Conversely, rather than selecting for overall genetic quality, females may be sexually attracted to males who have dissimilar genes than themselves, and exhibit mate choice for unrelated or unfamiliar males (Barbary macaques, *Macaca sylvanus*: Kuester et al., 1994; Japanese macaques, *M. fuscata*: Huffman, 1991; Takahata, 1982; Takahata et al., 1999; rhesus macaques, *M. mulatta*: Bercovitch, 1997; olive baboons, *Papio cynocephalus*: Packer, 1979a). Preference for novelty may ultimately function in

inbreeding avoidance (Pusey and Wolf, 1996). Social familiarity or unfamiliarity as well as olfactory cues indicative of genetic constitution (by which females may be able to judge relatedness) may be the proximal mechanisms which enable incest avoidance by females. In reality, females may select for a certain male as a mate both because of the direct benefits the male may provide as well as for the male's genetic make-up, as these two categories are not mutually exclusive.

Male-Male Competition

In addition to female mate choice, the outcome of mating also depends upon some form of male-male mating competition. The most salient form of intra-sexual male mating competition is physically combative competition among males (Clutton-Brock et al., 1979). In as far as females are a monopolizable resource (Emlen and Oring, 1977), males should use a combative strategy, and aggressively attempt to defend reproductive females (or the territory they use) from other males (Clutton-Brock and Harvey, 1977). Conversely, male-male reproductive competition may take a more subtle, non-overtly aggressive form, such as sperm competition (Parker, 1970) or sneak copulations (Berard et al., 1994). Non-aggressive male mating strategies are most frequently found where females (or the resources that they use) cannot be monopolized, and scramble competition (whereby resources are gained on a first-come, first-served basis) prevails.

Hence, two broad classes of male mating strategies can be identified: physically combative strategies requiring the use or threat of aggression, and non-combative mating strategies. Importantly, some mating systems are a mixture of both scramble and contest

competition, which often creates a situation where multiple mating strategies are present in a population simultaneously, and males can use a number of alternative strategies (Gross, 1996; Jones and Agoramoorthy, 2003). Examples of combative male mating strategies in primates include physically aggressive contest competition with other males over access to sexually receptive females, such as occurs in the redtail monkey, *Cercopithecus ascanius* (Cords, 1984). Another combative male strategy involves aggression against infants in the form of sexually-selected infanticide (e.g., langurs, *Presbytis entellus*: Hrdy, 1974). Conversely, there are many male mating strategies in primates that do not depend on physical competition among males for mates, such as sneak copulations with females (gibbons, *Hylobates* spp.: Palombit, 1994), forming affiliative friendships with females (baboons, *Papio cynocephalus*: Strum, 1982; Smuts, 1985), or competing against other males via sperm competition (apes: Harcourt et al., 1981). Such non-physically aggressive strategies might be employed by all males in some species (e.g., muriquis, *Brachyteles arachnoides*: Strier, 1992), and only by some males within a population in other species (e.g., Japanese macaques, *Macaca fuscata*: Soltis et al., 1997).

Sexual Dimorphism Versus Sexual Monomorphism

Where male mating tactics requiring the threat or actual use of aggression are common, it would generally be expected that sexual dimorphism favoring large male body size would result. Indeed, where notable sexual dimorphism exists (with males having larger body size or larger canines than females), this sex difference is often

attributed to male-male competition in which large males have a mating advantage (Darwin, 1871; Crook and Gartlan, 1966; Gartlan, 1970; Crook, 1972). Also implicated in the evolution of sexual size dimorphism favoring larger male body size and weaponry is the importance of males in predator defense (DeVore and Washburn, 1963; Rowell and Chism, 1986). Empirical evidence from non-human primates suggests that protection against predators and sexual selection appear to have been important in the evolution of sexual dimorphism favoring large male body size and canines (Leutenegger and Kelly, 1977; Harvey et al., 1978; Clutton-Brock, 1985; Kay et al., 1988; Plavcan and van Schaik, 1992, 1997; Ford, 1994; Mitani et al., 1996; Plavcan, 1999, 2001).

However, one paradoxical finding in some non-human primates is the presence of male-male aggressive contest competition in the absence of sexual dimorphism and large male body size. Some members of one unique taxonomic group, the Malagasy lemurs (family Lemuridae), show aggressive male-male competition over mates, but virtually no sexual dimorphism (Kappeler, 1990b). Although there are some exceptions in which members of one sex are larger (i.e. brown lemur, *Eulemur fulvus rufus*: Johnson, 2002; Johnson et al., 2005; Coquerel's dwarf lemur, *Mirza coquereli*: Kappeler, 1997; sifaka, *Propithecus verreauxi verreauxi*: Lewis, 2004; Lewis and Kappeler, 2005; prosimians: Kappeler, 1991), many of the Malagasy lemurs lack body size or canine dimorphism (Kappeler, 1990b, 1991; Feistner and Sterling, 1995; Smith and Jungers, 1997; Sauther et al., 2001), a trait which is even shared by large-bodied extinct subfossil lemurs (Godfrey et al., 1993).

Several hypotheses have been suggested for the evolution of sexual size monomorphism in lemurs (Richard, 1992; Kappeler, 1993b; van Schaik and Kappeler, 1996; Wright, 1999). The various explanations include the suggestion that lemurs may be sexually monomorphic due to the majority of intra-sexual competition occurring via sperm competition (Kappeler, 1993b), or because there may be positive selection for traits important in male speed, agility, and locomotor performance rather than selection for large body size (Kappeler, 1990b, 1993b; Lawler et al., 2005). There is currently no consensus among researchers on the cause of sexual monomorphism in this taxonomic group. Nor have there been any studies comparing the mating and reproductive success of males using combative behavioral mating strategies versus alternative non-physically combative strategies in any lemur species. In addition to sexual size monomorphism, many lemurs also exhibit a social trait which is extremely rare among animals, female dominance over males (Jolly, 1966, 1984; Richard, 1987; Pereira et al., 1990; Kappeler, 1993a).

Female Dominance

In numerous animal species, male dominance over females predominates (Archer, 1988). Male dominance is often thought to be a by-product of intra-sexual selection for male aggression and large body size (Crook and Gartlan, 1966). Female dominance occurs when all females are able to consistently evoke submissive behavior from all males in dyadic agonistic interactions (Kappeler, 1993a). Few mammals exhibit female dominance, especially as this trait is strictly defined by Kappeler (1993a). The spotted

hyena, *Crocuta crocuta*, is often described as a female dominant species because there is evidence for female agonistic wins during feeding competition and female priority of access to feeding at carcasses (Kruuk, 1972; Tilson and Hamilton, 1984; Frank, 1986). However, despite the fact that female hyenas are heavier than (Hamilton et al., 1986) and more aggressive than males, female spotted hyenas do not consistently dominate males in all contexts (Frank et al., 1989; Smale et al., 1993).

True female dominance as defined by Kappeler (1993a) only exists among some of the Malagasy lemurs (Richard, 1987; Pereira et al., 1990). Evidence for female dominance has been found in the blue-eyed black lemur, *Eulemur macaco flavifrons* (Digby and Kahlenberg, 2002), Alaotran gentle lemur, *Hapalemur griseus alaotrensis* (Waeber and Hemelrijk, 2003) eastern lesser bamboo lemur, *H. g. griseus* (Grassi, 2001), indri, *Indri indri* (Pollock, 1979), ring-tailed lemur, *Lemur catta* (Jolly, 1966; Taylor and Sussman, 1985; Taylor, 1986; Kappeler, 1990a; Pereira et al., 1990; Sauther, 1992; Gould, 1994; Sauther et al., 1999), Milne-Edwards' sifaka, *Propithecus diadema edwardsi* (Pochron et al., 2003), Verreaux's sifaka, *P. verreauxi* (Richard and Heimbuch, 1975; Richard, 1978; Kubzdela et al., 1992; Brockman, 1994; Kubzdela, 1997), mouse lemur, *Microcebus murinus* (Radespiel and Zimmermann, 2001), and ruffed lemur, *Varecia variegata variegata* and *V. v. rubra* (Kaufman, 1991; Morland, 1993; Raps and White, 1995; Meyer et al., 1999).

Several adaptive hypotheses have been proposed for the evolution of female dominance in lemurs. One early hypothesis which considered male submission to females as an energy conservation mechanism suggested that female dominance may

have resulted from males saving up energy reserves for male-male competition (Hrdy, 1981). It has also been suggested that males defer to females, especially in feeding contexts, as a form of reproductive investment ensuring growth and survival of their offspring (Pollock, 1979; Jolly, 1984; Pochron et al., 2003), and that male submission may be a mating strategy for males (Pereira et al., 1990). Other adaptive explanations for female dominance include the energy frugality hypothesis, which suggests that female dominance evolved in association with a suite of other behavioral and life-history traits (such as territoriality, cathemerality, and weaning synchrony) to compensate for the unpredictable food supply and harsh environmental conditions in Madagascar (Wright, 1999). Given the extreme seasonality of food resources in Madagascar, female dominance may enable males to inhabit social groups with females (thereby providing services such as predator detection or defense) without imposing a high cost of feeding competition via their subordinate status in the group (Sauther, 1993). The high cost of reproduction for female lemurs figures largely in many adaptive explanations for the evolution of female dominance (Jolly, 1984; Richard and Nicoll, 1987; Young et al., 1990; Pereira, 1993b), and leads some authors to conclude that female dominance allows female lemurs in Madagascar to avoid reproductive stress (Pereira et al., 1999).

Within a female dominant species, mating dynamics might be expected to differ greatly compared to primate species where males are dominant. For example, male sexual coercion of females – which can include male abuse of females and forced copulation – are commonly found among many anthropoid primates showing male dominance (Smuts and Smuts, 1993; Clutton-Brock and Parker, 1995). Male sexual

coercion might be expected to be entirely absent in female dominant primates due to males' inability to aggressively dominate females in such species. Another expectation in female dominant species is that females should have free choice of mates (Pereira and Weiss, 1991). To evaluate these expectations about the mating dynamics of a female dominant primate, the ringtailed lemur (*Lemur catta*) was selected as a study species for this multi-year project, which specifically investigated female mate choice and male mating strategies.

This Study: Sexual Selection in the Ring-tailed Lemur (*Lemur catta*)

Both components of sexual selection were investigated as part of this study: intra-sexual selection (male-male mating competition), and inter-sexual selection (female mate choice). A multi-year behavioral study spanning five consecutive breeding seasons from 2000-2005 was conducted to: 1) identify mating strategies used by males and measure their relative frequency and success, and 2) investigate variables potentially important in female mate choice, specifically male dominance status, male age, and residence status (familiarity).

The location selected for this study, St. Catherines Island[1] (Georgia, USA) was specifically chosen for its open habitat and favorable observation conditions. For a history of the *L. catta* colony at this location, see Keith-Lucas et al. (1999) and Parga and Lessnau (2005). For a history of St. Catherines Island, refer to Thomas et al. (1978) and Thomas (1988). The favorable observation conditions at this site were expected to

[1] The official name of the island lacks an apostrophe.

markedly increase the quality of data collected on *L. catta* mating behavior by allowing the determination of such details as the occurrence of ejaculation during copulatory mounts. In addition, the managing organization of the primate colony, the Wildlife Conservation Society, provided information on matrilineal relatedness among individuals since the colony's inception, and furnished data on male inter-troop movement in the colony since 1997, which greatly increased the explanatory power of this study.

L. catta: An Ideal Subject for the Study of Mating in a Female Dominant Species

L. catta is an ideal study subject for an investigation of the mating strategies in a group-living mammal showing female dominance. *L. catta* live in multi-male, multi-female groups with 1:1 sex ratios, in which both males and females can mate with multiple members of the opposite sex (Jolly, 1966; Sussman, 1974, 1991; Budnitz and Dainis, 1975; Mertl-Milhollen et al., 1979; Jolly et al., 1982b; Taylor, 1986; Koyama, 1988; Pereira and Weiss, 1991; Sauther, 1991; Gould, 1994, 1996; Gould et al., 2003; Pride, 2003, 2005). Whereas only some prosimians exhibit female dominance (Pereira et al., 1990), and other non-primate mammals exhibit female dominance in only certain contexts (i.e., hyenas, *Crocuta crocuta*: Frank et al., 1989; Smale et al., 1993), *L. catta* was chosen for this particular project because there is abundant evidence for female dominance in both feeding and non-feeding contexts (Jolly, 1966; Taylor and Sussman, 1985; Taylor, 1986; Kappeler, 1990a; Pereira et al., 1990; Sauther, 1992; Gould, 1994; Sauther et al., 1999).

Furthermore, studying a species such as *L. catta* with a temporally well-defined (rather than continuous or prolonged) period of sexual receptivity (Nadler, 1994) helps to remove ambiguity about which copulations occur during periods of fertility. In most mammals it is difficult, if not impossible, to determine the time of conception under free-ranging conditions, even when fecal or urinary samples are collected to help determine the hormonal status of females (Campbell, 2004). As a result, it is often unknown which observed copulations corresponded with periods of potential conception, making the evolutionary effects of observed mate choice behaviors and mating strategies difficult to interpret.

Moreover, some primates can be sexually receptive for days or even weeks during their peri-ovulatory periods (Martin, 1992) and often mate when conception is unlikely or impossible due to pregnancy or anovulation (e.g. Manson et al., 1997). However, reproduction in *L. catta* is strictly seasonal (Jolly, 1984; Rasmussen, 1985), and mating only lasts one day (Jolly, 1966, 1967; Evans and Goy, 1968; Van Horn and Resko, 1977; Koyama, 1988; Sauther, 1991; Koyama et al., 2001; Pereira and Weiss, 1991). Because each copulation can potentially lead to fertilization in *L. catta*, all observed copulations have the potential to affect male reproductive success, which is ultimately important to evolution. Among day-active lemurs, *L. catta* also have short estrus periods which last for less than one day in length, whereas other lemurs can show sexual receptivity across a longer 2-4 day period (i.e., Verreaux's sifaka, *Propithecus verreauxi*: Brockman, 1999; black and white ruffed lemurs, *Varecia variegata variegata*: Morland, 1993). The much more temporally-constrained mating period of *L. catta* allows a researcher to know more

definitively the entire sequence of a female's mates (which is important for estimating male mating success), because there is a higher likelihood of observing a shorter estrus period in its entirety.

L. catta female estrus periods are also typically non-overlapping with those of other females in a social group (Pereira, 1991; Sauther, 1991), which means that researchers only need to focus on a single mating female per social group at a time. *L. catta* are also largely terrestrial (Jolly, 1966; Sussman, 1974), increasing the likelihood of observing copulations and the social dynamics surrounding mating. For these reasons, *L. catta* is an ideal study species for an investigation of mating behavior in a female dominant primate.

The Ring-tailed Lemur, *Lemur catta*: Previous Research and Unanswered Questions

In addition to being an ideal study subject for investigating the mating dynamics in a female dominant primate, there are currently many unanswered questions surrounding the sexual behavior of this primate species. Previous research documenting *L. catta* mating behavior has shown a fair amount of variability with respect to the types of males preferred by females. Though some studies found that females often mated first with dominant troop males (Koyama, 1988; Sauther, 1991; Sauther and Sussman, 1993), females have been observed mating with both lower-ranking and extra-group males in the wild (Jolly, 1966; Budnitz and Dainis, 1975; Sauther, 1991; Sussman, 1992; Gould, 1994, 1996), and novel males have been observed to be preferred mates in captivity (Pereira and Weiss, 1991). Though variability in female choice is evident based on these studies,

only a multi-year study with a large sample size of estrus females and observed matings can explain typical trends in female choice and male mating strategies across time.

Furthermore, though previous studies have reported that *L. catta* females can mate with more than one male during estrus (Taylor, 1986; Koyama, 1988; Pereira and Weiss, 1991; Sauther, 1991; Sussman, 1992; Sauther and Sussman, 1993; Gould, 1994, 1996), it is currently unknown how extensive multiple mating is in this species (i.e., what the average number of mates is per female). Also currently unknown is whether male inter-troop transfer is a successful strategy by which a male can increase his mating success. Unfortunately, because all previous studies were only conducted across 1-2 breeding seasons each, it is difficult to generalize across studies to identify which characteristics sexually preferred males share, or which behavioral mating strategies used by male *L. catta* are most successful. Hence, one of the aims of this dissertation is to provide a multi-year view of mating patterns in a single population of *L. catta*.

The Question of Sexual Monomorphism in *Lemur catta*

Data on female choice and male sexual strategies in *L. catta* can help to elucidate the paradox between levels of male-male competition and sexual size monomorphism in some primates. Despite intense male-male aggressive competition during mating periods (Jolly, 1966; Taylor, 1986; Koyama, 1988; Pereira and Weiss, 1991; Sauther, 1991; Gould, 1994; Cavigelli and Pereira, 2000; Gould et al., 2005; Parga, 2006), *L. catta* exhibits sexual monomorphism in both body size (Kappeler, 1990b) and dentition (Sauther et al., 2001). It is therefore important to identify the different mating strategies

used by males, quantify their frequency of use, and measure the success gained by males using each type of strategy. Accordingly, data on the relative success of physically combative versus alternative non-combative male mating strategies are needed.

One untested possibility is that male physically aggressive strategies are not successful in conferring mating or reproductive success on males as compared to non-combative strategies. Only behavioral measures can indicate which strategies are being employed, the frequency with which each is used, and which types of individuals use each mating strategy. With the aid of molecular genetic analyses (Di Fiore, 2003; Di Fiore and Gagneux, 2007), data on paternity can then be used to indicate which behavioral mating strategies result in fertilization success. Together with paternity data, behavioral data will help to determine the relative importance of male aggressive contest competition in this and other species lacking sexual monomorphism.

The results of this study will therefore contribute markedly to knowledge about the types and frequencies with which different male mating strategies are used in *L. catta*, and will help determine the relative importance of male-male physical combat versus alternative mating tactics to male mating success. The investigation of alternative reproductive tactics is a subject of adamant investigation in current studies of sexual selection both within primatology (e.g. Berard et al., 1994), and more broadly, within animal behavior at large (e.g. Neff, 2001).

Dissertation Overview

Chapter 2 investigates the relationship between male dominance rank and male mating success, and tests whether male *L. catta* on St. Catherines Island have priority of access to estrus females. Chapter 3 examines the dynamics surrounding the disruption of male dominance hierarchies during the mating season, and provides a preliminary explanation for rank reversals among males during estrus periods. Chapter 4 reviews male inter-troop movement patterns on St. Catherines Island, and compares these patterns to male migration behavior in the wild. This chapter also evaluates the relationship between male inter-troop transfer and male mating success. Chapter 5 considers female mate choice in *L. catta*, and tests different male variables (dominance rank, age, and tenure status) to identify which male characteristics best predict patterns of female mate choice. Chapter 6 is a case study of one yearling female who experienced male sexual coercion during her estrus period. This dissertation concludes with Chapter 7, which summarizes major findings presented in the dissertation.

CHAPTER 2: MALE DOMINANCE STATUS AND MALE MATING SUCCESS

INTRODUCTION

Agonistic Dominance

Social dominance is the ability to win consistently in agonistic conflicts with other individuals (Hand, 1986). Though there are many different ways of defining and measuring dominance (Rowell, 1974; Bernstein, 1981; de Waal, 1989; Drews, 1993), dominance is generally regarded as conferring priority of access to resources (Clutton-Brock and Harvey, 1976). Because sexually receptive females are an important limiting resource for males (Bateman, 1948; Trivers, 1972), it is often expected that dominant males should have greater mating and reproductive success than subordinate males (Bernstein, 1976). Indeed, in numerous animal species, including invertebrates, fish, reptiles, birds and many mammals, there is evidence that dominant males (those with high social status) frequently have higher mating and reproductive success than do non-dominant individuals (Dewsbury, 1982; Fedigan, 1983; Cowlishaw and Dunbar, 1991; Ellis, 1995).

Priority of Access Model

In primatology, early attempts to model the relationship between dominance rank and mating success among male primates included the "priority of access" model proposed by Altmann (1962). This model was developed by Altmann using data from

Carpenter's (1942) study of rhesus macaques (*Macaca mulatta*) on Cayo Santiago, Puerto Rico, and attempted to explain patterns of sexual behavior among multi-male primate groups with male dominance hierarchies. Among the Cayo Santiago macaques, there was a positive relationship between male dominance status and access to sexually receptive females. Consequently, Altmann's (1962) model predicted that a single highest-ranking male would monopolize cycling females during periovulatory days, *insofar as periods of sexual receptivity among females did not overlap*. According to the model, lower-ranking males would only gain mating opportunities if more than one female was sexually receptive simultaneously. In short, greater estrus synchrony among females was predicted to decrease the alpha male's ability to monopolize matings.

Though data from multi-male, dominance hierarchy-forming primate groups do not always perfectly fit Altmann's (1962) priority of access model, higher-ranking males in many anthropoid primate species tend to have higher mating and/or consortship success than other males (rhesus macaques, *Macaca mulatta*: Carpenter, 1942; Kaufmann, 1965; Conaway and Koford, 1964; Hill, 1987; bonobos, *Pan paniscus*: Kano, 1996; savannah baboons, *Papio cynocephalus*: Hausfater, 1975; Packer, 1979b; Sapolsky, 1983; Bulger, 1993). This positive association commonly found between male dominance status and mating success is even further supported by paternity data in many groups. High-ranking males father a greater proportion of infants than do non-dominant males, e.g. red howler monkey, *Alouatta seniculus* (Pope, 1990); sooty mangabeys, *Cercocebus torquatus atys*: Gust et al., 1998; long-tailed macaque, *Macaca fascicularis* (de Ruiter et al., 1992, 1994; de Ruiter and van Hooff, 1993); Japanese macaques, *M.*

fuscata (Soltis et al., 2001); rhesus macaques, *M. mulatta* (Smith, 1981, 1993); Barbary macaques, *M. sylvanus* (Paul et. al., 1993); mandrills, *Mandrillus sphinx* (Dixson et al., 1993; Charpentier et al., 2005); bonobo, *Pan pansicus* (Gerloff et al., 1999); common chimpanzee, *P. troglodytes* (Constable et al., 2001; Klinkova et al., 2005); savannah baboon, *Papio cynocephalus* (Altmann et al., 1996); langurs, *Semnopithecus entellus* (Launhardt et al., 2001).

However, in some of the very same species and populations in which a positive relationship between dominance status and male mating or reproductive success has been found, other studies reveal that a male's agonistic dominance status does not correlate with his mating, consortship, or reproductive success (vervet monkeys, *Cercopithecus aethiops*: Cheney et al., 1988; rhesus macaques, *Macaca mulatta*: Loy, 1971; Japanese macaques, *M. fuscata*: Takahata et al., 1999; Inoue et al., 1991, 1993; Berard et al., 1993; baboons, *Papio spp.*: Strum, 1982; Smuts, 1985; Bulger, 1993). Female mate choice for non-dominant males (e.g., Strum, 1982; Soltis et al., 1997) is commonly identified as a primary reason for the lack of support for the priority of access model. Female promiscuity (Small, 1990), the inability of dominant males to sequester females (e.g., Berenstain and Wade, 1983), the use of leverage by lower-ranking males (Lewis, 2002), and breeding seasonality (Paul, 1997) are all cited as factors which contribute to the lack of correspondence between a male's dominance rank and his mating success.

As is evident from the above-listed studies, there has been a predominance of research investigating the link between dominance status and mating and/or reproductive success among anthropoid primates. With a few exceptions, information on dominance

status and male mating performance is scant among prosimian primates. One reason for the scarcity of information on the relationship between male mating success and dominance status is that studies of this kind are confounded by several characteristics common to many prosimians: temporally short estrus periods (Jolly, 1966, 1967; Morland, 1993; Brockman, 1999), extremely small group sizes (Kappeler and Heymann, 1996) which result in limited explanatory power due to small sample size or total lack of observed copulations, low rates of agonism which make determination of dominance relationships among males difficult or impossible (Erhart et al., 2002), and widespread arboreality (Sussman, 1999), which decreases the likelihood that mating will be observed. In certain prosimian species, an analysis of a male's dominance status relative to other reproducing group males is not possible, as there is only one non-natal resident male per group (e.g., Alaotran gentle lemur, *Hapalemur griseus alaotrensis*: Nievergelt et al., 2002), while other groups are comprised of a monogamous male-female pair and their offspring (e.g., the red-bellied lemur, *Eulemur rubriventer*: Merenlender, 1993). Of the studies that have been able to investigate the relationship between male mating performance and dominance rank in multi-male prosimian groups, several have shown a positive association between male dominance status and mating (sifaka, *Propithecus verreauxi*: Brockman, 1999) and reproductive success (brown lemur, *Eulemur fulvus mayottensis*: Gachot-Neveu et al., 1999; redfronted lemur, *E. f. rufus*: Wimmer and Kappeler, 2002; grey mouse lemur, *Microcebus murinus*: Andres et al., 2001).

In one of the best-studied prosimians, the ringtailed lemur, *Lemur catta* (Jolly, 1966; Sauther et al., 1999), studies have shown that there can be much variability in the

outcome of mating dynamics with respect to male rank. Though Koyama (1988) and Sauther (1991) have found that high-ranking male *L. catta* tend to mate first with estrus females, researchers in the wild (Gould, 1994) and in captivity (Pereira and Weiss, 1991) have noted that dominant males are not always the first to copulate with females. Females can also frequently mate with multiple males during a single estrus period (Taylor, 1986; Koyama, 1988; Pereira and Weiss, 1991; Sauther, 1991; Sussman, 1992; Sauther and Sussman, 1993; Gould, 1994, 1996), including subordinate and extra-troop males (Jolly, 1966; Budnitz and Dainis, 1975; Sauther, 1991; Sussman, 1992; Gould, 1994, 1996). Each of these studies were conducted for one to two mating seasons in duration, with a limited sample size of estrus females and mating males. Therefore, there is no consensus on the typical pattern of mating in *L. catta*, nor is it known whether dominant males have superior reproductive success in this species.

Though the present study did not measure male reproductive success, this project was the first to examine the relationship between male mating success and male dominance status in *L. catta* across a multiple year period, using a larger sample size of males than previous investigations of mating behavior in this species. This study was also conducted at a different study site than the previously-mentioned projects, which had either been completed in the wild (Berenty: Jolly, 1966; Budnitz and Dainis, 1975; Koyama, 1988; Beza Mahafaly: Sauther, 1991; Sussman, 1992; Sauther and Sussman, 1993; Gould, 1994, 1996) or on semi-free-ranging *L. catta* in captivity (Duke Primate Center: Taylor, 1986; Pereira and Weiss, 1991). The present study was conducted on a

free-ranging provisioned population of *L. catta* on St. Catherines Island, Georgia, USA (Keith-Lucas et al., 1999; Parga and Lessnau, 2005).

Reproduction in *Lemur catta*

Like most Malagasy primates, *L. catta* breed seasonally (Jolly, 1984; Rasmussen, 1985). Because females are only sexually receptive during the peri-ovulatory period (also known as vaginal estrus: Evans and Goy, 1968; Van Horn and Resko, 1977), all copulations are potentially conceptive. There are no non-conceptive matings in this species, such as that which occurs in anthropoids (e.g. Manson et al., 1997). A single copulatory event can contain several separate mounts (some with and without intromission) before ejaculation is achieved, and males only ejaculate once with a female during a single estrus cycle (Sauther, 1991; Parga, 2003). *L. catta* can therefore be placed in category #10 (no copulatory lock, thrusting, multiple intromissions, single ejaculation) according to the schema devised by Dewsbury (1972) to describe mammalian mating patterns.

Each female's estrus period is short, lasting for approximately a day or less in duration (Jolly, 1966; Evans and Goy, 1968; Van Horn and Resko, 1977; Koyama, 1988; Sauther, 1991). Some estrus periods can be as short as three and a half hours (Koyama, 1988; Sauther, 1991; Parga, 2006). Females within a social group will cycle within one to three weeks of one another (Sauther, 1991), and captive studies indicate that female *L. catta* can cycle up to three times per season if kept under natural light conditions, with each cycle being separated by an average of 39 days (Evans and Goy, 1968). Though

females can cycle three times, most females who conceive do so during their first estrus cycle of the season (Sauther, 1991; Parga and Lessnau, 2005). Females also experience asynchronous estrus, which has been found in the wild (Sauther, 1991) and in captivity (Pereira, 1991). This estrus asynchrony should enable a single high-ranking male to monopolize copulations with each estrus *L. catta* female, upholding the predictions of Altmann's (1962) priority of access model.

This Study: Male Dominance and Mating Success

The first goal of the present study was to test whether the priority of access model (Altmann, 1962) was supported by data collected on female *L. catta* on St. Catherines Island. Altmann's model predicts that dominant males will monopolize copulations with sexually receptive females if there is no overlap in female estrus periods. Previous research suggests that dominant *L. catta* males are unable to monopolize matings, and that females mate multiply, i.e., with more than one male (Taylor, 1986; Koyama, 1988; Pereira and Weiss 1991; Sauther, 1991; Sussman, 1992; Sauther and Sussman, 1993; Gould, 1994, 1996). Even if dominant males are unable to monopolize estrus females, theory would still predict that these dominant males have higher mating and/or reproductive success than other males (Bernstein, 1976; Andersson, 1994). Therefore, the second goal of this study was to test for a positive relationship between male dominance status and male mating success in the St. Catherines Island *L. catta* population.

Because studies of *L. catta* have noted disruptions of the male dominance hierarchy during mating periods in both the wild (Jolly, 1966, 1967; Budnitz and Dainis, 1975; Koyama, 1988; Sauther, 1991; Gould, 1994, 1997; Sauther et al., 1999) and in captivity (Pereira and Kappeler, 1997), pre-breeding season male dominance ranks were used in this study. These dominance breakdowns can sometimes occur as distinct male dominance rank reversals. During dominance rank reversals, a lower-ranking male challenges and begins 'winning' in agonistic interactions over the alpha male (or other high-ranking male). Using this strategy, males ascend in dominance rank, and thereby gain access to the estrus female (Parga, 2002a, 2002b). These male rank reversals are the subject of Chapter 3.

METHODS

Study Site and Study Animals

The present study was conducted with four *L. catta* social groups on St. Catherines Island, GA, USA across a five-year period (Table 2.1). Provisioned, free-ranging *L. catta* groups have been maintained on St. Catherines Island (Thomas et al., 1978; Thomas, 1988) by the Wildlife Conservation Society since 1985 (Keith-Lucas et al., 1999). This site (located at 31º 40' N latitude, 80º 41' W longitude) is a privately-owned, largely undeveloped semi-tropical barrier island measuring 2,900 hectares, with a mixture of habitats, including pine, oak and palmetto forests, and open pastures as well as savanna and marsh (Keith-Lucas et al., 1999).

Keith-Lucas et al. (1999) provide a brief history of the *L. catta* colony on St. Catherines Island, including a description of lemur behavior following the initial release of six founder individuals. The lemurs on St. Catherines are provisioned daily with food (a mixture of monkey chow and fruits and/or vegetables), and water. The lemurs also forage on naturally-occurring vegetation, show ranging behaviors, and have established home range areas (Dierenfeld and McCann, 1999; Keith-Lucas et al., 1999). All adult lemurs have been fitted with uniquely-colored Telonics radio collars (Mesa, AZ). Subadults and small adults were often fitted with nylon collars. Differences in physical characteristics and shaving patterns were used to identify uncollared animals.

At one time, the *L. catta* colony on St. Catherines grew to over 75 individuals in four free-ranging groups (Parga and Lessnau, 2005). Each of these groups was studied across the duration of this project, though different groups were studied in each year. Table 2.1 shows the groups that were studied during the start and middle of the breeding season in each year of this project (spanning late October-December). Table 2.2 shows the composition of each study group in early October (just prior to the start of the mating season) of each year. Each lemur group had between 5-11 females one year of age or older, and 2-4 non-natal males one year of age or older (Table 2.2).

Data Collection on Mating and Social Behavior

A. Breeding Season

Due to photoperiodic regulation, reproduction among *L. catta* on St. Catherines is approximately six months out-of-phase with the timing of these events in Madagascar,

the endemic habitat of *L. catta* (Rasmussen, 1985). Mating behavior is limited to the fall and winter months (September-February) in the northern hemisphere if the lemurs are exposed to natural light (Evans and Goy, 1968; Van Horn, 1975). Data on mating behavior were collected during five consecutive breeding seasons: October-December 2000-2004, with additional data collected on mating behavior late in the breeding season of one year, during January-February 2004.

During breeding periods, data were collected daily from "dawn to dusk" using 'all-occurrences' sampling (Altmann, 1974) of agonism and reproductive behavior. In mating contexts, the following behaviors were recorded (in addition to recording the agonistic behaviors listed in section "B. Non-Breeding Season" below): jump-fights, mounts, thrusting, and female sexual presents. If observable, penile intromission, ejaculation, and copulatory plug displacement (Parga, 2003) were also recorded, though observation conditions did not always allow these more detailed sexual behaviors to be verified. Ejaculation was indicated by the presence of semen in the female's peri-vaginal area, and/or on the tip of the male's penis. The start time (and stop time, if appropriate) of each behavior was recorded in seconds. Behavioral estrus was indicated by proceptive (sexual solicitation) or receptive (allowance of male mounting) behavior (Beach, 1976).

During the 2001 through 2004 breeding seasons, one to two field assistants helped monitor groups for estrus behavior and collect social and reproductive data. One observer was stationed per group unless a female was in estrus in one of the groups, in which case two observers paired up at the group with the estrus female.

B. Non-Breeding Season

During the pre-breeding months of each year (June-September in 2000 and 2004, and September-October 2001–2003), data were collected on social behavior approximately five days per week between the hours of 0600 and 1900, with the majority of samples collected between 0800 and 1600. Information on dominance relationships among males was gathered during this time via two main sampling techniques: continuous-time focal animal sampling, and 'all-occurrences' sampling for agonism (Altmann, 1974). Each sampling technique was performed separately, alternating between the two sampling types throughout the day. Each type of sample lasted for 20 minutes during 2000-2001, and was thereafter shortened to 15 minutes in duration. Focal sampling order was randomized, with no more than two samples per individual per day.

During focal samples, the following 'state' behaviors (Martin and Bateson, 1986) were recorded to the nearest second: rest, travel, feed, auto-groom, and allo-groom. The following 'event' behaviors (Martin and Bateson, 1986) were scored: approach, defecate, urinate, scent-mark (ano-genital, palmar, shoulder, tail), approach-withdraw, bite, chase, cuff, fight, grapple, lunge, nose-push, push, stink-fight, and take food (Jolly, 1966; Petter and Charles-Dominique, 1979; Taylor, 1986; Gould, 1994; Pereira and Kappeler, 1997; Parga, 2002a). *Ad libitum* data were collected at all times during all seasons of the year in both non-mating and mating periods to record sporadic or infrequent events such as predation attempts on the lemurs, instances of mobbing, and alarm or howling vocalizations.

Definition of Mating, Male Mating Success, and Mate Guarding

Mating is defined here as a male mounting a female. A more detailed definition such as 'mounting with penile intromission' or 'mounting with ejaculation' was not used because observation conditions did not always permit documentation of penile intromission or ejaculation during mounts. Male mating success is defined as the number of females a male was observed mounting in a single mating season. Though male reproductive success (number of offspring sired) would be a more desirable measure than male mating success, paternity data are not available at the present. Male mate guarding specifically refers to the agonistic defense by a male of an individual female during all or part of her estrus period (Clutton-Brock, 1989a). Pre-copulatory mate guarding takes place prior to the male's first mount. Post-copulatory mate guarding takes place following the male's ejaculation.

Data Analysis

Only data from groups in which a clear male dominance hierarchy existed during the pre-breeding season of each year were used in analyses. Discussions of dominance throughout this work refer to dominance expressed as the outcome of agonistic interactions (de Waal, 1989). All "decided" agonistic interactions (Hausfater, 1975; Pereira and Kappeler, 1997) between males were used to construct the male dominance hierarchy within each group. Agonistic outcomes for each male dyad were tallied in a matrix, as described in Bramblett (1994). This method allows for a net dominance score

to be calculated for each individual and a corresponding rank to be assigned to each based upon their relative dominance score.

Two groups in two study years were identified as not having a discernable hierarchy: Group 1 in 2000, and Group 4 in 2004. Data from these groups were excluded from these analyses. Both were groups in which three of the four adult non-natal males present in the group were recent immigrants. In 2000, WCS personnel released three novel unrelated males into Group 1 just prior to the start of the breeding season in September. Male dominance relationships were too variable in the short period of time prior to mating to identify a hierarchy. In the spring of 2004, three males immigrated of their own accord into Group 4. Too few agonistic interactions between the immigrants and the resident male of the group (DA, Table 2.2) were recorded to determine a male dominance hierarchy. Mating dynamics and mate choice in these two troops are addressed in Chapter 5.

Because more than one season of data were collected on certain males in the study, values for male mating success and male dominance rank were averaged across different seasons such that each male only contributed a single data point in analyses. Analyses were performed using non-parametric statistics, including the Binomial test, Chi-square goodness of fit, Friedman's two-way ANOVA, Kruskal-Wallis one-way ANOVA, Mann-Whitney *U*, and Spearman rank correlation. All tests were two-tailed, and the significance level was set at 0.05. All means are reported with the standard error of the mean (SEM). Statistical tests were performed using Statistica, version 5.5.

RESULTS

Number of Mates Per Female

A total of 40 estrus periods were observed in which females mated with at least one male. These data resulted from 28 different females' estrus periods. Of these estrus periods, 30 were in groups with discernable male dominance hierarchies (Table 2.3). Fewer than half of these females (n = 12) were observed to mate with one male, whereas the remaining females mated with two to four males (Figure 2.1). There was no statistically significant difference in the numbers of females who mated with one male as opposed to two or more males (Binomial test, $p = 0.18$, NS).

For most females, only a portion of the estrus period was witnessed, which likely resulted in an underestimate of the number of male mates per female. In all cases where a female's entire estrus period was witnessed, the female mated with two or more males (Figure 2.1), making female multiple mating common.

Degree of Estrus Synchrony

In the majority of estrus periods observed (62.5%), only a single female was in estrus at a time. During November 2003, Group 3 had some estrus overlap during the receptive periods of five females, with two to three females in estrus simultaneously during four days of the breeding season. The two males present in this group were able to copulate simultaneously on two occasions by directing their mating efforts (e.g., attempted mounts) towards different females. However, in all other instances when more than one female was in estrus, the males challenged each other over the same female,

nullifying the effect of synchronous estrus. Hence, data from all seasons are pooled for the following analyses, as the ubiquitous pattern across all seasons was one of intense male-male competition over a single female.

Are Alpha Males Able to Monopolize Estrus Females?

Alpha males did not monopolize copulations with estrus females, and males of all dominance ranks mated (Figure 2.2; Table 2.3). The proportion of copulations performed by males of each dominance rank was not significantly different than what would be expected if males of different dominance ranks had mating success equal to their representation in the population (Chi-square goodness of fit: $\chi^2 = 0.301$, df = 3, $p < 0.96$, NS).

The percentage of copulations performed by males of each dominance rank also did not differ significantly depending on how many males each female copulated with during her estrus (Friedman's 2-way ANOVA: $\chi^2 = 5$, df = 3, $p < 0.172$, NS; Figure 2.3). Therefore, even among females who were witnessed mating with just one or two males, non-alpha males were frequently their observed mating partners (Figure 2.3).

Do Dominant Males Have Higher Mating Success Than Other Males?

An analysis of each male's mating success per season compared with his dominance rank shows that dominant males were no more likely to mate with a larger proportion of estrus females than were lower-ranking males (Spearman rank correlation: $r_S = 0.061$, n = 27, p = 0.761, NS). If the number of females mated is used in the analysis

instead of the proportion of females mated, male mating success and male dominance rank are still not correlated (Spearman rank correlation: $r_S = 0.093$, n = 27, p = 0.643, NS). Averaging values for male mating success and male dominance rank across different seasons such that each male only contributes a single data point, there is no correlation between mean proportion of estrus females mated and mean male dominance rank (Spearman rank correlation: $r_S = 0.182$, n = 14, p = 0.534, NS; Figure 2.4). If the mean number of females mated is used as a measure of male mating success in the analysis instead of the mean proportion of females mated, mean male mating success and mean male dominance rank are still not correlated (Spearman rank correlation: $r_S = 0.140$, n = 14, p = 0.632, NS; Figure 2.5).

Male Mate Guarding

Observation conditions allowed documentation of male behavior prior to the male's first mount in 49 separate mating pairs. In most cases (n = 43), males did not pre-copulatory guard, but instead began mate guarding activities following their first mount. Where pre-copulatory mate guarding was documented (n = 6), individual male guarding durations ranged between three and twelve minutes, with an overall mean of 7.0 ± 1.5 minutes across all males. Males of all dominance ranks except delta were observed to pre-copulatory mate guard.

Post-copulatory mate guarding following a male's ejaculation was much more frequent than pre-copulatory guarding. In 35 instances in which there was an opportunity to document post-copulatory mate guarding, males post-copulatory guarded in 25 cases.

Where males showed post-copulatory mate guarding behavior, individual male durations of guarding ranged between 2 and 199 minutes, with an overall mean of 28.5 ± 8.1 minutes across all males.

Because the number of other male competitors in the group might be expected to affect a male's ability to mate guard, male post-copulatory mate guarding durations were analyzed with respect to the number of non-natal male group members present at the time of the female's estrus. There was not a significant correlation between the number of other non-natal males present in a group and male post-copulatory mate guarding duration (Spearman rank correlation: $r_S = -0.268$, $n = 35$, $p = 0.119$, NS).

Male post-copulatory mate guarding duration also did not correlate with male age (Spearman rank correlation: $r_S = 0.052$, $n = 35$, $p = 0.768$, NS) or with male dominance rank (Spearman rank correlation: $r_S = -0.266$, $n = 35$, $p = 0.123$, NS). Repeating this analysis using a single mean value for age, dominance rank and post-guarding duration per male, male post-copulatory guarding duration still did not correlate with male age (Spearman rank correlation: $r_S = 0.127$, $n = 14$, $p = 0.666$, NS) or with male dominance rank (Spearman rank correlation: $r_S = -0.077$, $n = 14$, $p = 0.793$, NS).

Furthermore, though beta males exhibited a broader range of mean guarding durations (Figure 2.6), there was no significant difference in post-copulatory mate guarding durations across dominance rank categories (Kruskal Wallis one-way ANOVA: $\chi^2 = 5.73$, $df = 3$, $p = 0.126$, NS), which means that alpha males as a group did not guard for significantly longer periods of time than did other males (Figure 2.6). Multiple values

for the same male within the same dominance rank category were averaged so that each male contributed a single data point per dominance rank.

An overall analysis of male post-copulatory mate guarding duration and male mating order (irrespective of dominance rank) shows that there is no statistically significant difference in the post-copulatory mate guarding durations of males mating at different places in the mating queue (Kruskal-Wallis one-way ANOVA: $\chi^2 = 0.472$, df = 3, p = 0.925, NS; Figure 2.7).

Though not all alpha males (or first-mating males) mate guarded for longer periods of time than did other males following ejaculation, one alpha male in particular who was the first to ejaculate multiple different times (BY, Table 2.3) tended to consistently post-copulatory mate guard for longer periods of time than did subsequent mates (Figure 2.8a), as might be expected. However, other alpha males who were also first to mount and/or ejaculate (ED and CP, Table 2.3) failed to show this trend of mate guarding for longer periods than subsequent mates (Figure 2.8b). As these graphs show, there is much inter-individual variability in male mate guarding behavior, even among males of the same dominance rank.

Other Mating Strategies: Dominance Rank Reversals, Evasion, and Sneak Copulations

In addition to the aggressive mating strategy of rank reversal, subordinate males practiced two additional alternative mating strategies that can be considered 'aggression avoidance' strategies: sneak copulation and evasion (Table 2.3). During sneak copulations, males copulate out of view of higher-ranking males. In evasion copulations,

the male copulates in full view of higher-ranking males, but does so when his competitors are physically distant enough to not be an immediate threat. When higher-ranking males were observed to move closer to evading males, these males attempted to avoid contact with the alpha male, even when this led to their loss of proximity to the estrus female. Different alternative male mating strategies were not employed with equal frequency (Chi-square goodness of fit: $\chi^2 = 25.8$, df = 2, $p < 0.0001$). Rank reversal was the most commonly used male mating strategy, employed in 70.7% of copulations achieved by non-alpha males, and 45.3% of total copulations performed by all males (Figure 2.9). Non-alpha males of all dominance ranks used the rank reversal strategy more frequently than they used other alternative mating strategies (Figure 2.10).

Both evasion and sneak copulations occurred infrequently (Table 2.3). Even if counted together, these two strategies occurred less often than did the rank reversal mating strategy (Chi-square goodness of fit: $\chi^2 = 7.05$, df = 1, $p < 0.008$; Figure 2.9). Fewer males practiced sneak copulations than evasion. Whereas all six evasions were performed by different males, three of the six cases of sneak copulation were performed by the same one year old male in a single mating season (Table 2.3).

Male Mating Order

The start of estrus (indicated by proceptive or receptive female behavior) was witnessed 17 times during the estrus periods of 13 different females. An analysis of all copulations in which male mount order and male dominance rank was known (n = 36) showed that males tended to mount in the order of their rank (Figure 2.11). Furthermore,

male dominance rank and mount order were positively correlated (Spearman rank correlation: $r_S = 0.345$, $p = 0.04$). Alpha males in particular were significantly more likely to mount earlier in the queue than males of other ranks (Mann-Whitney: $n_1 = 13$, $n_2 = 23$, $U = 85.5$, $p = 0.034$; Figure 2.12). In fourteen cases where observation conditions allowed documentation of the first male to mount at the start of estrus, alpha males were the first to mount nine times (Binomial test, $p < 0.018$).

With respect to ejaculation, males also tended to ejaculate in the order of their rank (Spearman rank correlation: $r_S = 0.479$, $n = 24$, $p = 0.018$; Figure 2.13). Alpha males were significantly more likely to ejaculate earlier in the mating queue than other males (Mann-Whitney: $n_1 = 9$, $n_2 = 15$, $U = 29.0$, $p = 0.021$; Figure 2.14). In fact, in eleven cases where observation conditions allowed documentation of the first male to ejaculate, alpha males were first to ejaculate seven times (Binomial test, $p < 0.014$).

DISCUSSION

Male Dominance Rank Correlates with Male Mating Order, Not Male Mating Success

The operational sex ratio, which is the ratio of males to available breeding females in a group (Emlen and Oring, 1977), is highly skewed in this species due to the multi-male membership of *L. catta* groups and the nearly ubiquitous estrus asynchrony among females (Pereira, 1991; Sauther, 1991). Typically, the greater the degree of skew in the operational sex ratio, the higher the expected degree of reproductive skew (Clutton-Brock, 1998) among members of the limited sex. Because estrus is both asynchronous and extremely short in this species (Jolly, 1966; Evans and Goy, 1968; Van Horn and

Resko, 1977; Koyama, 1988; Pereira, 1991; Sauther, 1991; Parga, 2006), the alpha male of each group is expected to be able to monopolize each estrus female and sire all group infants, resulting in strong reproductive skew.

Though the vast majority of females experienced asynchronous estrus in this study, alpha males were unable to monopolize matings. Though some females were observed to mate only with the alpha male, the entire estrus period was not observed in these cases, casting doubt that the alpha male was her only mate. Notably, each female who was observed throughout her entire estrus period mated with at least two males, and there was widespread female multiple mating. Hence, the predictions of the priority of access model (Altmann, 1962) did not hold for cases in which a single female was in estrus per group.

The predictions of the priority of access model (Altmann, 1962) were also not consistently met where more than one group female was in estrus simultaneously in the same group, as occurred in Group 3 during 2003. Although both group males were able to copulate simultaneously by directing their mating attention to two different females on two separate occasions, during other female estrus periods these males came into direct conflict over a single female (even though at least one other group female was in estrus at the same time). In short, the predictions of the priority of access model (Altmann, 1962) were not supported in this *L. catta* population, as dominant males were unable to monopolize matings with estrus females.

However, data gathered on male mating order shows that alpha males were significantly more likely to be females' first-mates and were significantly more likely

than other males to first inseminate the female. Therefore, high-ranking *L. catta* males may be described as having priority of access to females, just not to the extent predicted by the priority of access model (Altmann, 1962). Patterns of female promiscuity documented in this study resembled that of previous *L. catta* studies at other sites, in which females have been observed mating with more than one male during estrus (Taylor, 1986; Koyama, 1988; Pereira and Weiss, 1991; Sauther, 1991; Sussman, 1992; Sauther and Sussman, 1993; Gould, 1994, 1996).

In the present study, a male's pre-breeding season dominance rank was not a strong predictor of his mating success (the number of females mated or the proprortion of group estrus females mated). Though female estrus cycles were typically non-overlapping in this study, the resultant patterns of mating in *L. catta* resembled primate species in which dominant males are unable to monopolize estrus females due to estrus synchrony. Paul (1997) has established that in seasonally breeding primates where multiple females are simultaneously sexually receptive, dominant males are often unable to monopolize females. In such cases, there is frequently no positive relationship between male dominance rank and reproductive success (Paul, 1997).

Male *L. catta*: Limited Defense of Estrus Females

In a long-term study of savannah baboons, *Papio cynocephalus*, Alberts et al. (2003) found that as the number of group males increased, male dominance rank was less likely to predict mating success. Similarly, in a comprehensive review of male dominance rank and male mating success in primates, Cowlishaw and Dunbar (1991)

concluded that although high-ranking males generally tend to have greater access to estrus females, the greater numbers of male competitors in large groups can compromise male monopolization potential. Though the *L. catta* groups in this study had relatively few males per group (between two and four), it appeared that no alpha male was able to defend estrus females from other males throughout the estrus period.

Alpha males might be expected to mate guard longer following ejaculation than males of other dominance ranks, especially as dominance status is frequently considered to signal "good genes" (Andersson, 1994). Although one particular alpha male (BY) in this study was observed to mate guard longer than subsequent mates, there was no statistically significant difference between the mate guarding durations of males of different dominance ranks in this study, because not all alphas showed longer post-copulatory mate guarding than other males. Even among alpha males who mate guarded for longer periods of time than did later-mating males, full monopolization of the estrus female was not possible, and mate guarding duration was limited.

One consequence for alpha males of this limited mate guarding was loss of proximity to the estrus female. The cessation of mate guarding most frequently occurred via dominance rank reversal, whereby males 'lost' in agonistic interactions with males who had been previously subordinate to them during the pre-breeding season (Chapter 3). Though temporary, the reversal of pre-breeding season dominance rankings resulted in non-alpha males gaining proximity to the estrus female, which created an opportunity for these males to mate without having to perform sneak or evasive copulations.

Mate guarding has been identified as a costly behavior for some male primates (e.g., baboons, *Papio cynocephalus*: Alberts et al., 1996; golden lion tamarins, *Leontopithecus rosalia*: Dietz et al., 1994; rhesus macaques, *Macaca mulatta*: Bercovitch, 1997; Japanese macaques, *M. fuscata*: Matsubara, 2003), as it can decrease time spent foraging and in so doing, lower overall energy intake, as well as require participation in energetically-expensive male-male agonistic competition. Similarly, mate guarding by *L. catta* males (Sauther, 1991) is likely an energetically expensive task, with costs deriving from male-male contest competition. Mate guarding requires continued vigilance and constant defense of the estrus female (Sauther, 1991; Sauther et al., 1999). Frequent male-male aggression such as chases, lunges and jump-fights are common during *L. catta* mating periods (Jolly, 1966; Taylor, 1986; Koyama, 1988; Pereira and Weiss, 1991; Sauther 1991; Gould, 1994; Gould et al., 2005; Parga, 2006). Males can incur wounds and serious injuries (Gould, 1994, 1997; Sauther, 1991), and visibly lose weight in the wild (Sauther, 1991) and in captivity (Pereira, 1993b) during the mating season. Because the first estrus cycle of the season is typically one to three weeks long (Sauther, 1991), mate guarding several females during this time can be energetically expensive, which may explain why males in this study only mate guarded for a limited time during any single female's estrus period.

The difficulty of mate guarding can be exacerbated by female approaches to competitor males and/or female aggression towards the guarding male (Chapter 3). Also, because of female dominance (Jolly, 1966; Taylor and Sussman, 1985; Taylor, 1986; Kappeler, 1990a; Pereira et al., 1990; Sauther, 1992; Gould, 1994; Sauther et al., 1999)

and sexual monomorphism in size and dentition (Kappeler, 1990b; Sauther et al., 2001), *L. catta* males cannot physically control adult female behavior via coercive tactics used by other primate males, including herding (i.e, hamadryas baboons, *Papio hamadryas*: Kummer, 1968; Swedell, 2006) and male aggression towards females (e.g., rhesus macaques, *Macaca mulatta*: Manson, 1994).

Comparison with Wild *L. catta* Studies

In Sauther's (1991) study of mating behavior of two groups of *L. catta* in Beza Mahafaly, Madagascar, the alpha male of each troop was the first observed mate in every instance of mating (six estrus females). Gould (pers. comm.) has also noted that high-ranking males are able to monopolize and sequester females for a large majority of time during their estrus. From these observations, it appears that high-ranking males in the wild may have greater monopolization potential than do high-ranking males on St. Catherines. In the present study, alpha males were significantly more likely to be the first to mount and ejaculate with estrus females, though not all alpha males consistently mate guarded females for a longer period of time than did other males. Males of all dominance ranks were observed to be the first mates of females on occasion, and there were alternative male mating strategies used, such as sneak and evasive copulations, which resulted in incomplete monopolization of the estrus female by alpha males.

The greater amount of variability observed on St. Catherines in the rank status of first mating males when compared to the studies of Koyama (1998) and Sauther (1991) may be simply due to a larger sample size of estrus females observed in the present study.

It is quite possible that studies of *L. catta* mating behavior in the wild with larger sample sizes of estrus females would reveal equal diversity in the identities of first-mating males. In fact, a number of authors studying wild *L. catta* (Jolly, 1966; Budnitz and Dainis, 1975; Sauther, 1991; Sussman, 1992; Gould, 1994, 1996) have noted that both lower-ranking and non-troop males mate with estrus females, so neither do high-ranking *L. catta* males in the wild have total monopolization ability over females in estrus. One important ecological difference between St. Catherines and the wild worthy of mention, however, is a major difference in food availability between the two locations. Due to the daily food provisioning on St. Catherines, non-alpha males at this site may be in much better physical condition than is typical for lower-ranking males in the wild, which may make lower-ranked males on St. Catherines more physically able to challenge alpha males. One testable hypothesis is that rank reversals among male *L. catta* on St. Catherines might be more frequent than among males in the wild. Ultimately, an assessment of male paternity from both locations would provide a true quantitative test of the reproductive success of alpha males versus males of all other dominance ranks at both localities.

Evasions and Sneak Copulations

In addition to rank reversal, evasive and sneak copulations by non-alpha males contribute to the inability of alpha males to monopolize matings with estrus females. Males employing these non-combative tactics gain the opportunity to mate without incurring the costs of male-male aggressive competition. Very few sneak copulations

were achieved across the multiple years of this study, which may indicate that sneak copulations are difficult for males to achieve. All group members show intense interest in the copulatory activities of an estrus female and her mate (Parga, pers. obs.), which likely decreases possibilities for sneak copulations. It appears that sneak copulations are performed opportunistically, because some males were observed to use this 'aggression avoidance' strategy only once (e.g., male MN in 2001). Though male MN's first documented copulation of the season was a sneak copulation, when subsequent females came into estrus, this male switched to the rank reversal strategy.

Males in this study who performed 'aggression avoidance' strategies such as sneak copulation and evasion were of all ages and belonged to all non-alpha rankings. However, a one-year-old male (MX) particularly took advantage of sneak copulations as a mating strategy. Paternity analyses are not yet completed on this population to evaluate whether his copulations led to fertilization, but it is known that male *L. catta* can reach puberty (as determined by the presence of descended testicles and the onset of genital scent marking) as early as 15 months in provisioned captive populations (Pereira, 1993a), and 20 months of age in the wild (Sauther, unpub. data). Male MX was the youngest male observed to ejaculate in this study, and was a yearling (20 months) at the time of his first mating season. It is therefore possible that this young male's use of sneak copulation may have gained him some degree of reproductive success, because three of the four females with whom he mated actually conceived during the observed estrus period. Each of the females who conceived also mated with at least one other male during the same

estrus period, precluding any definite knowledge of paternity in the absence of genetic data.

It is not surprising that a yearling male would elect to use an aggression avoidance mating strategy such as sneak copulation. Young males of several primate species opportunistically take advantage of sneak copulations (e.g., gibbons, *Hylobates* spp.: Palombit, 1994; Barbary macaques, *Macaca sylvanus*: Kuester and Paul, 1992; hamadryas baboons, *Papio hamadryas*: Kummer, 1968). This non-combative mating strategy is more conservative, and is likely safer than engaging in aggressive combat with adult males who are older, larger, and more experienced at male-male combat. Evasive and sneak copulations may primarily be used by males who have few other options (i.e. males who are not willing to use another more potentially costly strategy, such as rank reversal). Additionally, because in six of the seven cases of sneak copulation males mated with females who had already been previously inseminated by another male, it does not appear that sneak copulation allows males to ejaculate first in the mating queue. Ejaculating first may be important if there is a fertilization advantage earlier-mating males in this species.

Alpha Males Mating First: Implications for Male Reproductive Success

Male mating order in *L. catta* does not always correlate with dominance status in the wild (Gould, 1994) or in captivity (Pereira and Weiss, 1991). However, no study has heretofore analyzed male mating order by male dominance rank in *L. catta* using multiple years of data and a large sample size of estrus females. In this study, though alpha males

did not always mate first, males tended to mate in the order of their dominance status, and high-ranking males were often the first to mate to ejaculation with females. Sauther (1991) found the same pattern of high-ranking males mating first in her study, which took place across a single mating season in Beza Mahafaly, Madagascar. As the present study shows, alpha males, though not able to fully monopolize matings, were highly successful at mating first with the estrus female. This strategy of mating first (even if females proceed to mate with other males subsequently) may be critically important in sperm competition (Parker, 1970).

Sperm competition occurs when the sperm of one or more males compete to fertilize the same egg(s) (Parker, 1970; Birkhead and Moller, 1992). As suggested by Pereira and Weiss (1991), a first-male fertilization advantage (first male sperm precedence) may exist in *L. catta*. This hypothesis is supported by the discovery that the presence of semen in the *L. catta* female vaginal tract significantly shortens the period of sexual receptivity (Evans and Goy, 1968). Therefore, because alpha males in particular are significantly more likely than lower-ranking males to ejaculate earlier in the mating queue, alpha males may have greater reproductive success than other males despite the fact that they do not monopolize estrus females.

Sperm competition has been suggested as a causal factor in cases where male mating success does not correlate with male reproductive success. In Barbary macaques, *Macaca sylvanus*, Paul et al. (1993) found that although low mating success was always related to low reproductive success, males with high mating success could sometimes have low reproductive success, a difference attributed to sperm competition (see also

Inoue et al., 1993). A number of factors may influence male fertilization success via sperm competition: the latency between inseminations (Huck et al., 1985), the differential fertilizing capacity of different males' sperm (Lanier et al., 1979), differences in sperm number (sperm count), sperm motility, or sperm morphology (Freund, 1962), and differences in ejaculate volume or sperm plug volume (Parga et al., 2006). Particularly important to this study is whether mating order affects paternity in *L. catta*, or whether male reproductive success patterns suggest a 'fair raffle' (Parker, 1990), whereby each male's probability of reproductive success correlates with the number of sperm he inseminates. With the availability of paternity data, future research on reproduction in this population will test the relative importance of sperm competition in *L. catta*.

CONCLUSIONS

The priority of access model (Altmann, 1962) is based upon the assumption that male-male agonistic competition for mates is the primary mechanism by which males are able to monopolize matings with sexually receptive females. However, the model largely ignores the role of both female mate choice (Chapter 4) and alternative male mating strategies such as sneak and evasive copulations. In this study, a combination of 1) males' willingness to challenge higher-ranking males (via rank reversal), 2) male avoidance of aggression during mating (via evasions and sneak copulations), and 3) female multiple mating (promiscuity) nullified male monopolization potential.

Though the predictions of the priority of access model (Altmann, 1962) were not supported by data collected on *L. catta* in this study, attaining high dominance status in a

group and maintaining it throughout the weeks leading to the breeding season may still benefit a male, because alpha males are often the first to mount and inseminate estrus females. As a result, though alpha males may not have sole access to estrus females, they do appear to have some priority over mating first, and consequently may have higher reproductive success than other males if there is first-male sperm precedence (e.g. Foltz and Schwagmeyer, 1989) in *L. catta*.

However, many non-dominant males also mate and commonly displace the sperm plugs of previous mates prior to ejaculating (Parga, 2003). Sperm plug displacement may disrupt the fertilization success of previously-mating males by affecting the semen transport through the female's vaginal tract (Matthews and Adler, 1977), or by causing semen flowback, which plugs may help to prevent (Mann and Lutwak-Mann, 1951; Voss, 1979; Michener, 1984). In addition, the conspicuous post-copulatory mate guarding that occurs in this species (Sauther, 1991; Parga, this study) indicates that there is the potential for fertilization by later-mating males. Therefore, full reproductive skew favoring dominant males is not expected. Non-alpha males probably show some degree of reproductive success. Future genetic analyses will address whether male mating order determines fertilization success, and whether males with high dominance status have higher reproductive success than other males, as this study suggests.

Table 2.1: Study groups which were the focus of data collection on mating behavior in each year

Study year	Group 1	Group 2	Group 3	Group 4
2000	X		X	
2001	X		X	
2002	-	X	X	
2003	-	X	X	
2004	-		X	X

Note: In October 2002, Group 1 was removed from the colony for management purposes.

Table 2.2: Composition of each study group in each year

Study year	Study group	Females	Ages	Males	Ages	Natality of male
2000	1	LB	12	EK	2	Non-natal
		JL	4	FD	10	Non-natal
		KY	2	JY	1	Natal
		BT	3	RK	3	Non-natal
		HP	7	SP	4	Non-natal
	3	RR	11	BY	5	Non-natal
		MA	6	ED	9	Non-natal
		JN	4	BR	2	Natal
		JK	3	MC	13	Non-natal
		AN	2	CH	1	Natal
		JA	1	RY	1	Natal
		UR	10	DG	1	Natal
		LS	6			
		EB	2			
2001	1	LB	13	EK	3	Non-natal
		JL	5	FD	11	Non-natal
		KY	3	JY	2	Natal
		BT	4	RK	4	Non-natal
		HP	8	SP	5	Non-natal
		TA	1			
		AM	1			
	3	RR	12	BY	6	Non-natal
		MA	7	MC	14	Non-natal
		JN	5	MN	2	Non-natal

Table 2.2 (continued): Composition of each study group in each year

		JK	4	KL	8	Non-natal
		AN	3	DA	1	Natal
		JA	2	LE	1	Natal
				DG	2	Natal
2002	2	VN	8	ED	11	Non-natal
		QU	12	BR	4	Non-natal
		VT	4	CH	3	Non-natal
		JO	4	RY	3	Non-natal
		SHL	3	CP	1	Natal
		KA	1			
		TO	1			
		NI	2			
	3	RR	13	BY	7	Non-natal
		MA	8	MN	3	Non-natal
		JN	6	KL	9	Non-natal
		JK*	5	WD	1	Natal
		AN*	4			
		JA*	3			
		CA	1			
2003	2	JO	5	ED	12	Non-natal
		SHL	4	BR	5	Non-natal
		KA	2	RY	4	Non-natal
		TO	2	CP	2	Natal
		NI	3	FZ	1	Natal
		MY	1	MX	1	Natal
				LE	3	Non-natal
	3	RR	14	MN	4	Non-natal
		MA	9	KL	10	Non-natal
		JN	7	GR	1	Natal
		JK	6	DN	1	Natal
		AN	5	SB	1	Natal
		JA	4			
		CA	2			
		RA	2			
		ME	1			
		FR	1			
		DB	1			

* These 3 females were contracepted with a melengestrol acetate hormonal implant during the 2002 breeding season

Table 2.2 (continued): Composition of each study group in each year

2004	3	MA	10	MN	5	Non-natal
		JN	8	KL	11	Non-natal
		RA	3			
		FR	2			
		DB	2			
		HO	1			
	4	MG	9	DA	4	Non-natal
		NW	10	BR	6	Non-natal
		ND	6	ED	13	Non-natal
		SHR	6	FZ	2	Non-natal
		KY	2	TD	1	Natal
		RO	2	GA	1	Natal
		KT	2			
		SU	2			

Table 2.3: List of all mating pairs in groups having a pre-breeding season male dominance hierarchy

Year	Group	Estrus female	Male	Male mounting order	Order of ejaculation	Male dominance rank	Mating strategy used
2000	3	UR	BY	1	1	1	Alpha
		LS	ED	Unknown	Unknown	2	Rank reversal
		MA	BY	1	1	1	Alpha
		MA	ED	2	Unknown	2	Rank reversal
		JN	ED	Unknown	Unknown	2	Rank reversal
		AN	ED	Unknown	Unknown	2	Evasion
2001	3	JA	MN	1	1	3	Sneak
		JA	KL	2	2	2	Rank reversal
		MA	BY	2	1	1	Alpha
		MA	KL	1	2	2	Rank reversal
		MA	MN	3	3	3	Rank reversal
		RR	BY	1	1	1	Alpha
		RR	KL	3	2	2	Rank reversal
		RR	MN	2	3	3	Rank reversal
		RR	MC	4	4	4	Rank reversal
		JN	KL	Unknown	Unknown	2	Sneak
	1	KY	SP	Unknown	Unknown	1	Alpha
		KY	FD	Unknown	Unknown	3	Rank reversal
		KY	EK	Unknown	Unknown	2	Rank reversal
		JL	SP	Unknown	Unknown	1	Alpha
		JL	FD	Unknown	Unknown	3	Rank reversal
		JL	EK	Unknown	Unknown	2	Rank reversal
2002	2	SHL	BR	Unknown	Unknown	2	Rank reversal
		SHL	CH	Unknown	Unknown	4	Rank reversal
		SHL	RY	Unknown	Unknown	3	Rank reversal
		SHL	ED	Unknown	Unknown	1	Alpha
		JO	ED	1	1	1	Alpha
		JO	BR	2	2	2	Rank reversal
		JO	CH	3	Unknown	4	Rank reversal
		JO	RY	4	Unknown	3	Rank reversal
		QU	CH	Unknown	Unknown	4	Evasion
		QU	RY	Unknown	Unknown	3	Evasion
		VT	RY	Unknown	Unknown	3	Sneak
		VT	CH	Unknown	Unknown	4	Rank reversal
		TO	CH	1	Unknown	4	Rank reversal
		TO	RY	2	Unknown	3	Rank reversal
		TO	BR	3	Unknown	2	Rank reversal
		TO	ED	4	Unknown	1	Alpha

Table 2.3 (continued): List of all mating pairs in groups having a pre-breeding season male dominance hierarchy

	3	MA	MN	1	1	2	Unknown
		MA	KL	2	2	1	Unknown
		MA	BY	3	3	3	Unknown
		CA	KL	1	2	1	Alpha
		CA	BY	2	1	3	Rank reversal
		CA	MN	3	Unknown	2	Rank reversal
2003	2	MY	LE	Unknown	Unknown	4	Evasion
		TO	RY	1	2	3	Evasion
		TO	LE	2	1	4	Rank reversal
		TO	ED	3	Unknown	2	Evasion
		TO	BR	4	Unknown	1	Alpha
		KA	RY	Unknown	Unknown	3	Rank reversal
		KA	LE	Unknown	Unknown	4	Rank reversal
	3	JN	CP	1	1	1	Alpha
		JN	MX	2	2	2	Sneak
		MA	CP	1	1	1	Alpha
		RR	CP	Unknown	Unknown	1	Alpha
		AN	MX	Unknown	Unknown	2	Sneak
		RA	CP	1	Unknown	1	Alpha
		RA	MX	2	Unknown	2	Sneak
		JA	MN	Unknown	Unknown	3	Rank reversal
		MA	KL	Unknown	Unknown	2	Unknown
		MA	CP	Unknown	Unknown	1	Unknown
		MA	MX	Unknown	Unknown	4	Unknown
2004	3	JN	MN	Unknown	Unknown	2	Unknown
		HO	KL	1	1	1	Alpha

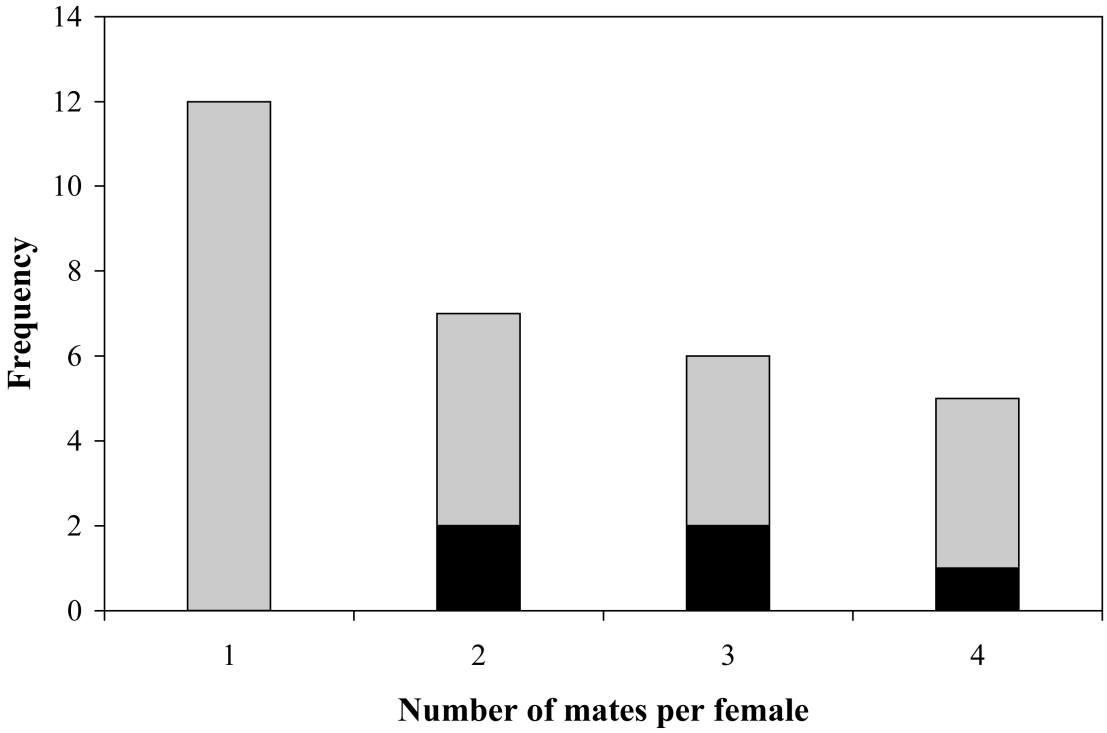

Figure 2.1: The number of observed mates per female. This graph represents the number of observed mates per female in groups having a male dominance hierarchy at the start of the mating period (n = 30). Black bars represent females for whom the entire estrus period was witnessed.

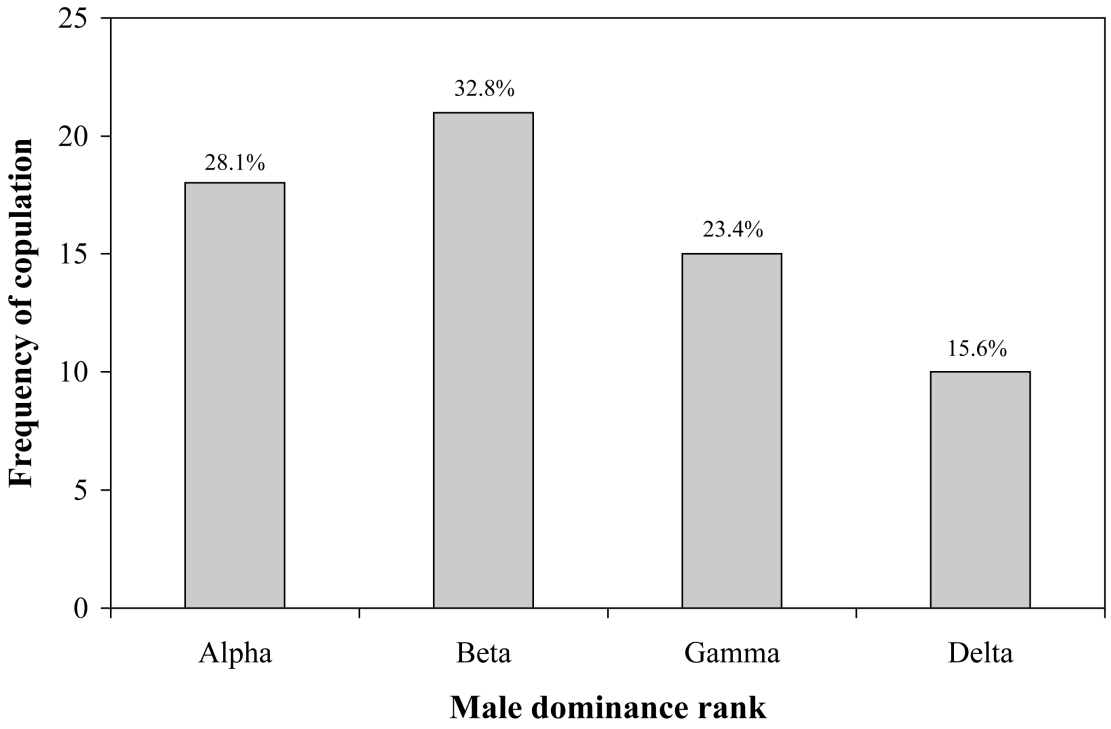

Figure 2.2: The frequency of copulation by males of each dominance rank. The frequency of copulation by males of each dominance rank did not differ significantly (Chi square goodness of fit: $\chi^2 = 0.301$, df = 3, $p < 0.96$, NS; n = 64 copulations).

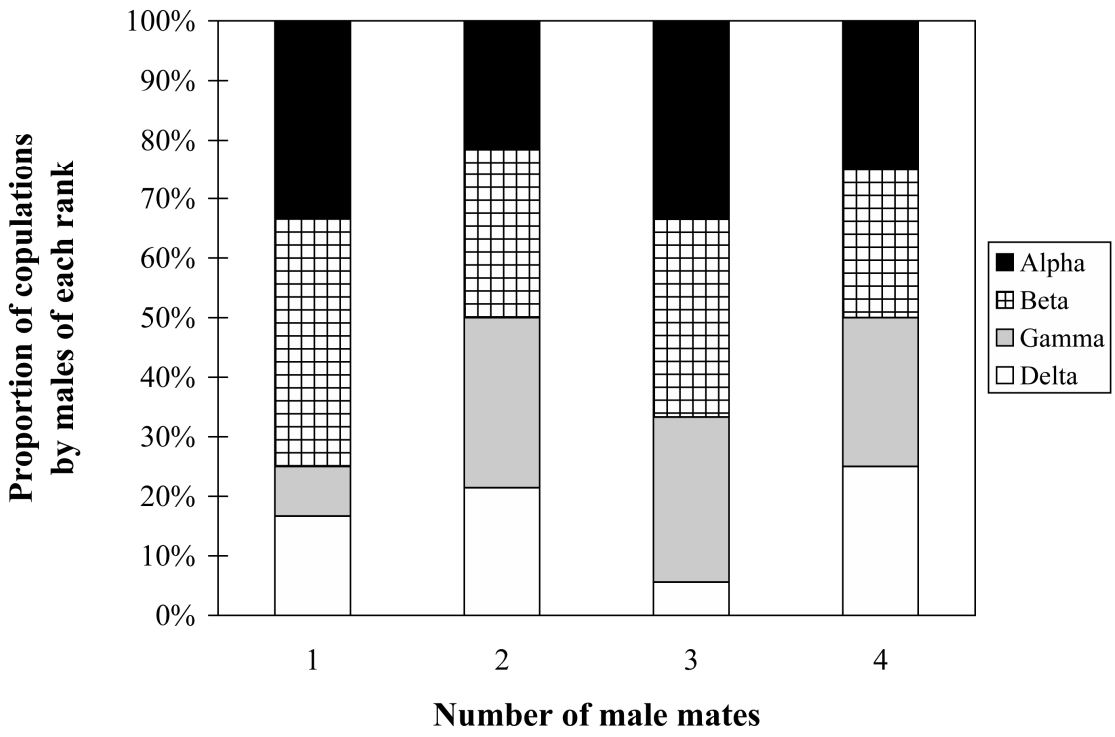

Figure 2.3: The proportion of copulations performed by males of each rank. The proportion of copulations performed by males of each rank did not significantly differ depending on the number of observed mates per female (Friedman's 2-way ANOVA: $\chi^2 = 5$, df = 3, $p < 0.172$, NS).

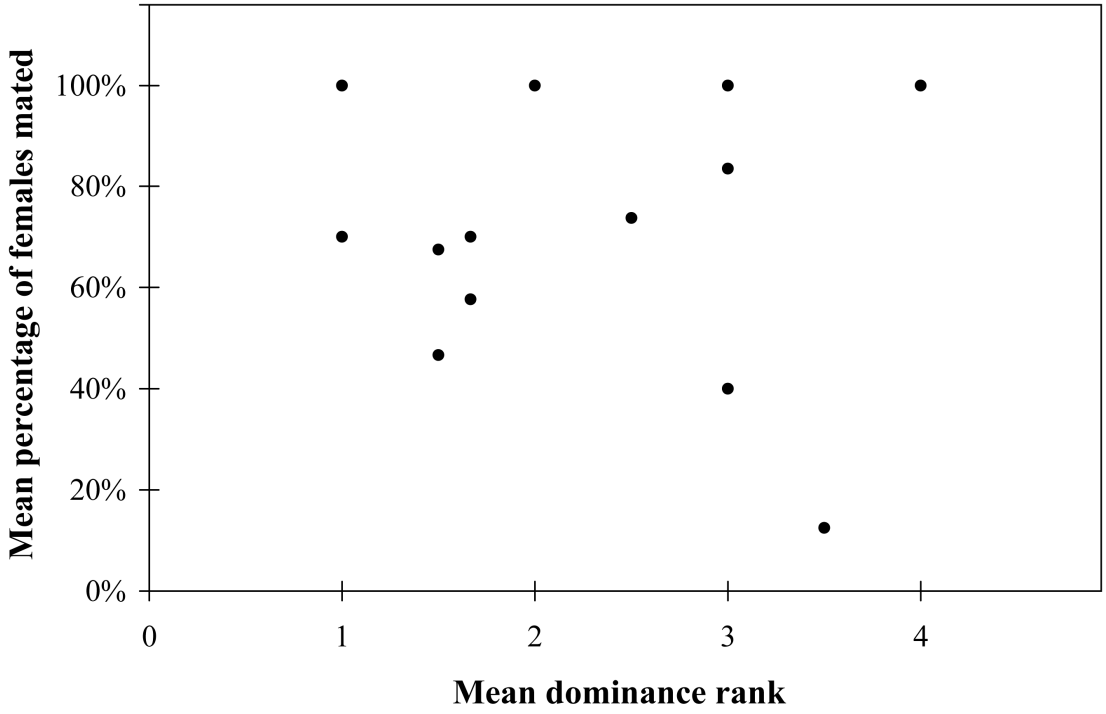

Figure 2.4: Mean percentage of females mated by mean male dominance rank. Mean male dominance rank did not correlate with mean percentage of estrus group females mated (Spearman rank correlation: $r_S = 0.182$, n = 14, p = 0.534, NS).

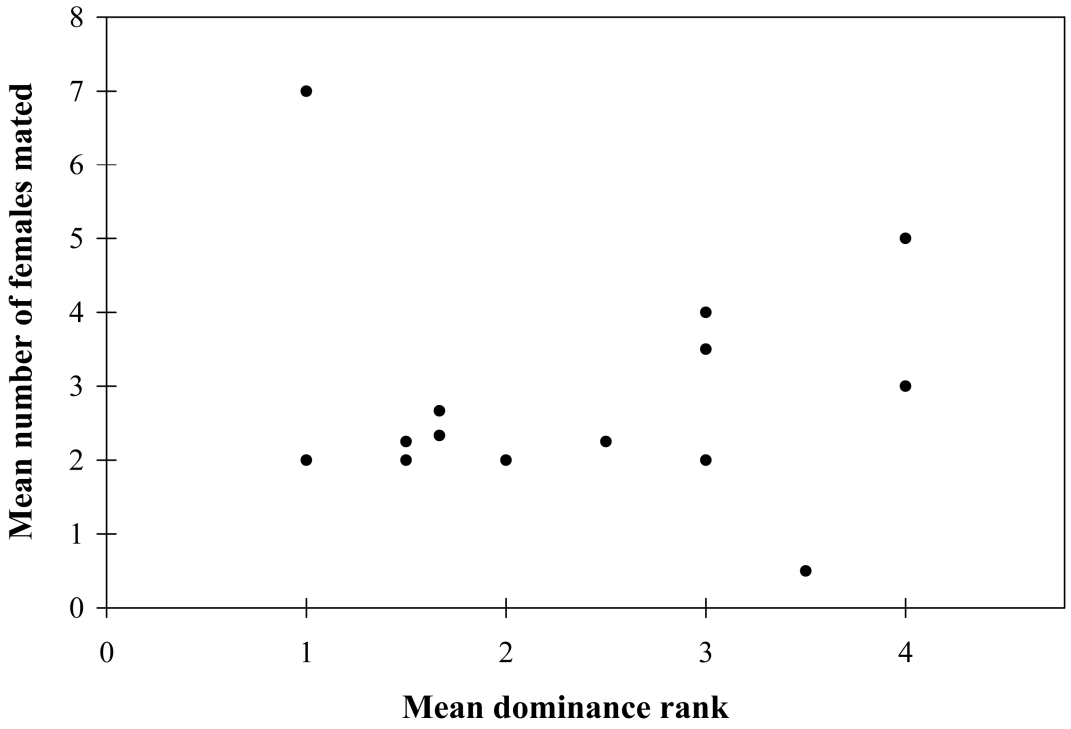

Figure 2.5: Mean number of females mated by mean male dominance rank. Mean male dominance rank did not correlate with mean number of females mated (Spearman rank correlation: $r_S = 0.140$, n = 14, p = 0.632, NS).

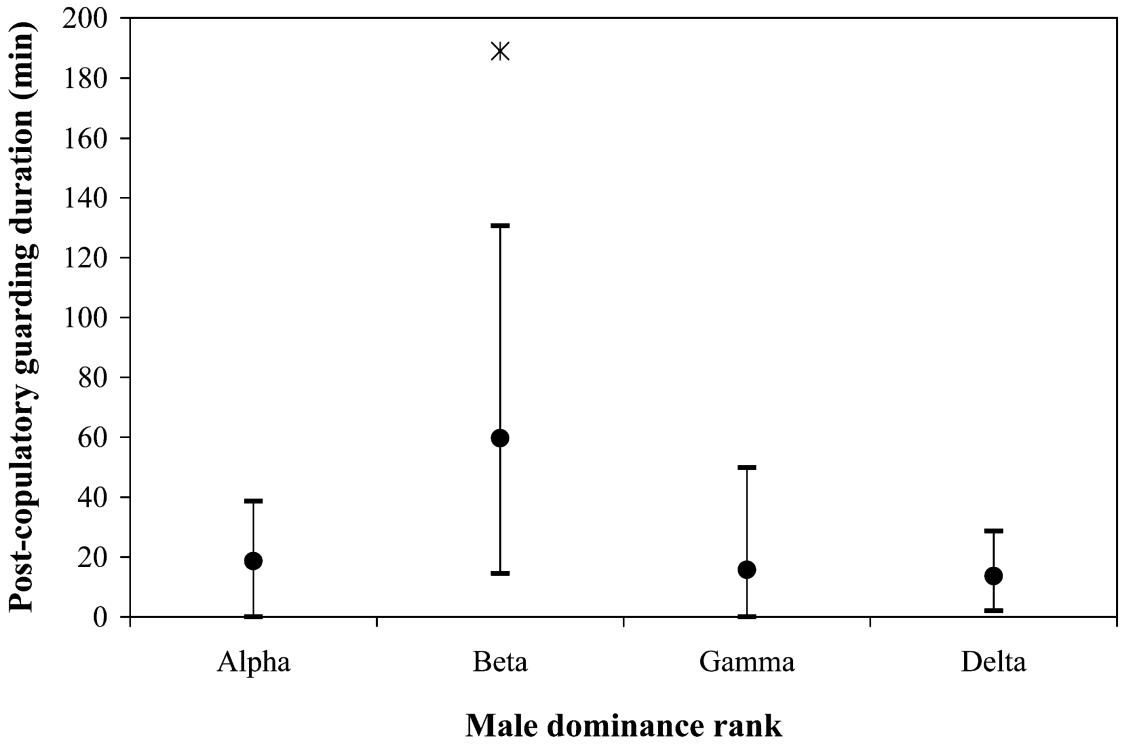

Figure 2.6: Male post-copulatory mate guarding duration by male dominance rank. There was no significant difference in post-copulatory mate guarding duration by males of different dominance ranks (Kruskal Wallis: $\chi^2 = 5.73$, df = 3, $n_{alpha} = 5$, $n_{beta} = 5$, $n_{gamma} = 4$, $n_{delta} = 3$, p = 0.126, NS). Maximum, minimum, and mean values are indicated for each rank. The asterisk denotes an outlier.

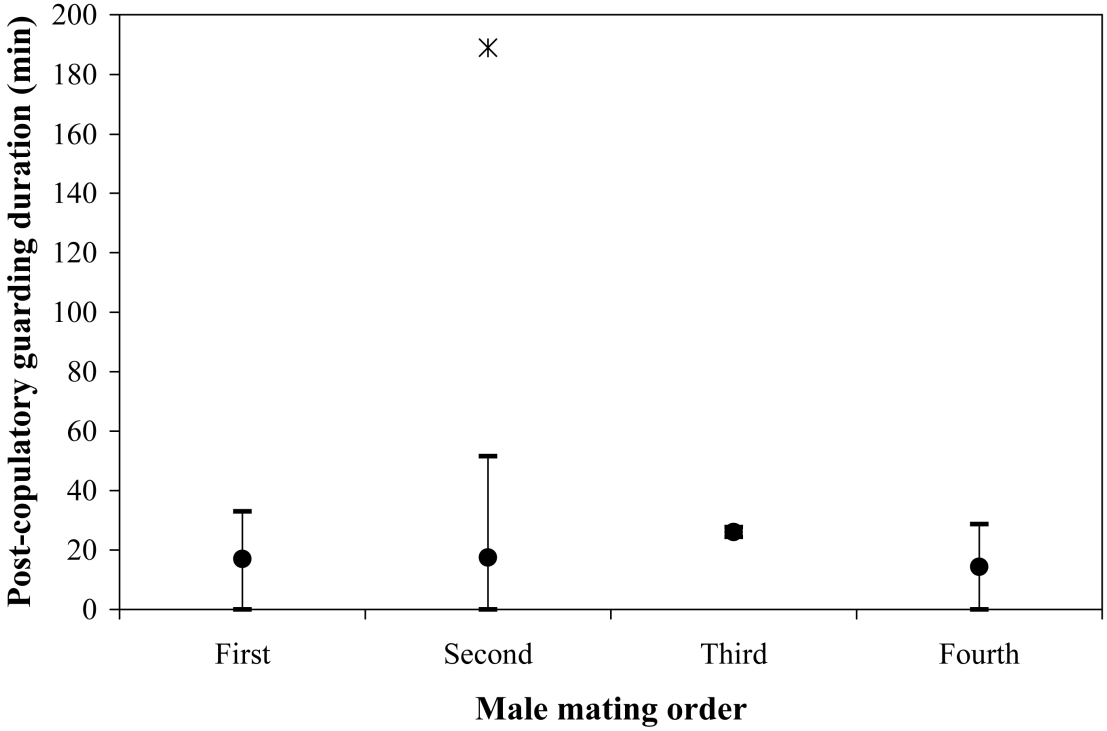

Figure 2.7: Male post-copulatory mate guarding duration by male mating order. There was no significant difference in post-copulatory mate guarding duration by male mating order (Kruskal Wallis: $\chi^2 = 0.472$, df = 3, $n_{first} = 5$, $n_{second} = 6$, $n_{third} = 2$, $n_{fourth} = 2$, p = 0.925, NS). Maximum, minimum, and mean values are indicated for each rank. The asterisk denotes an outlier.

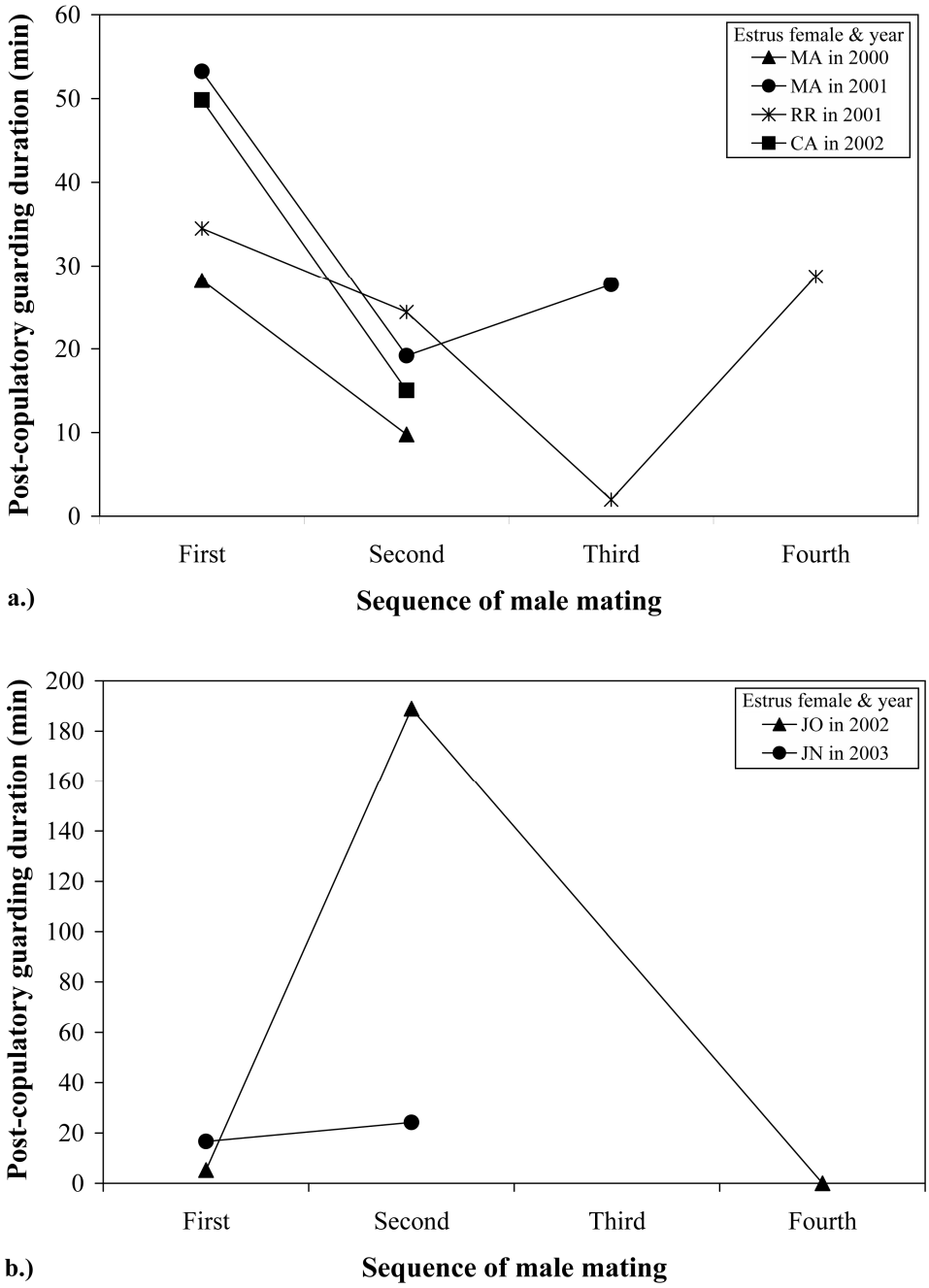

Figure 2.8: Examples of male post-copulatory mate guarding duration by mating order. Instances in which two or more males mated, post-copulatory guarding durations were known, and mounting and/or ejaculation order was known for a.) copulations in which the first male to ejaculate was male BY, and b.) copulations in which other alpha males (ED and CP) were the first to ejaculate. Though male BY mate guards for longer periods of time than do subsequent males, the same trend does not hold for other alpha males.

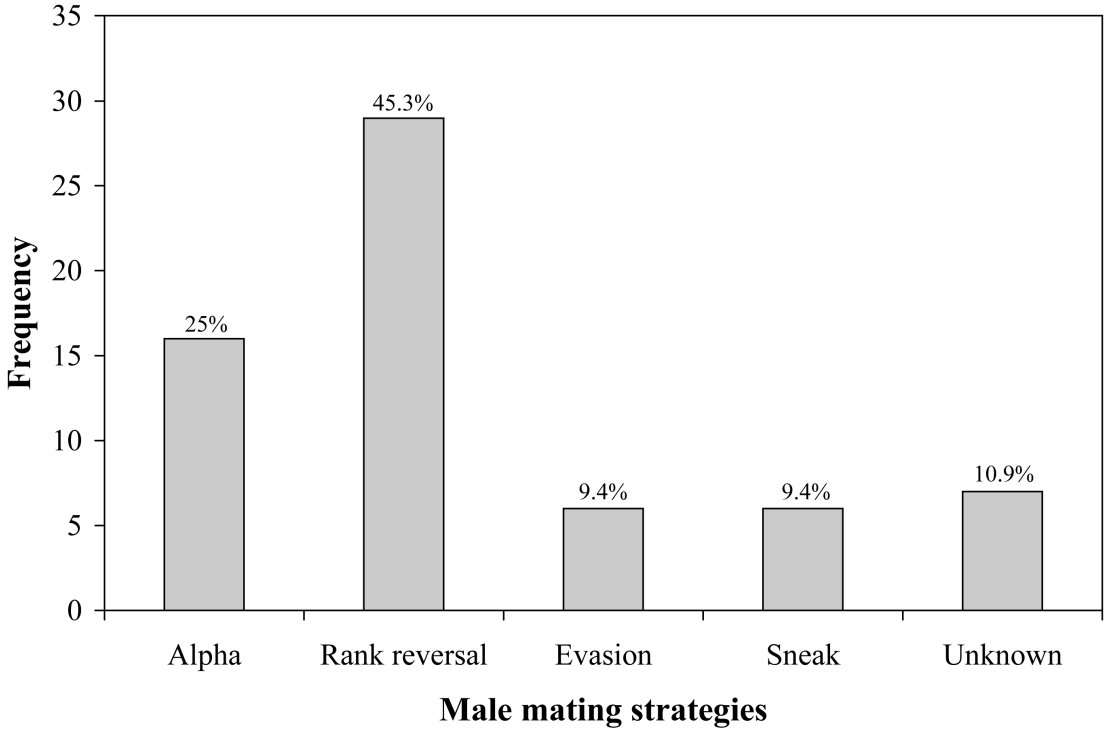

Figure 2.9: Male mating strategies used and their frequency.

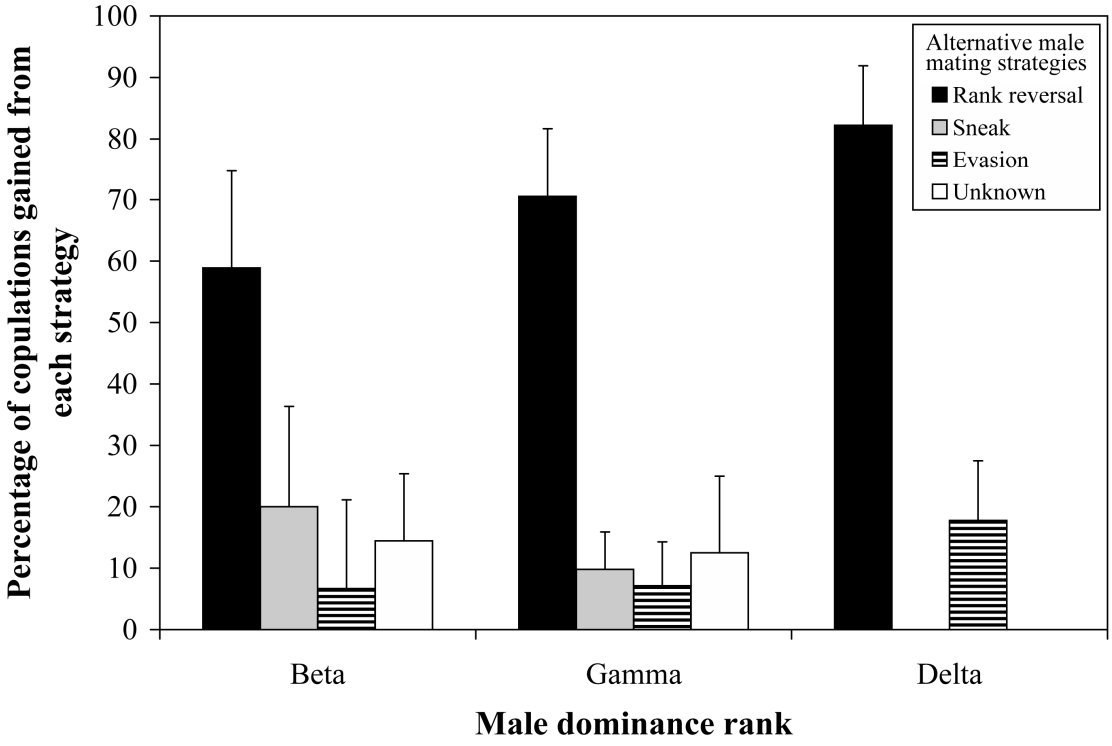

Figure 2.10: Alternative mating strategies used by non-alpha males. The percentage of copulations gained by non-alpha males using each type of alternative mating strategy are graphed here. Rank reversals were the most frequently used alternative male mating strategy for males within all non-alpha dominance ranks.

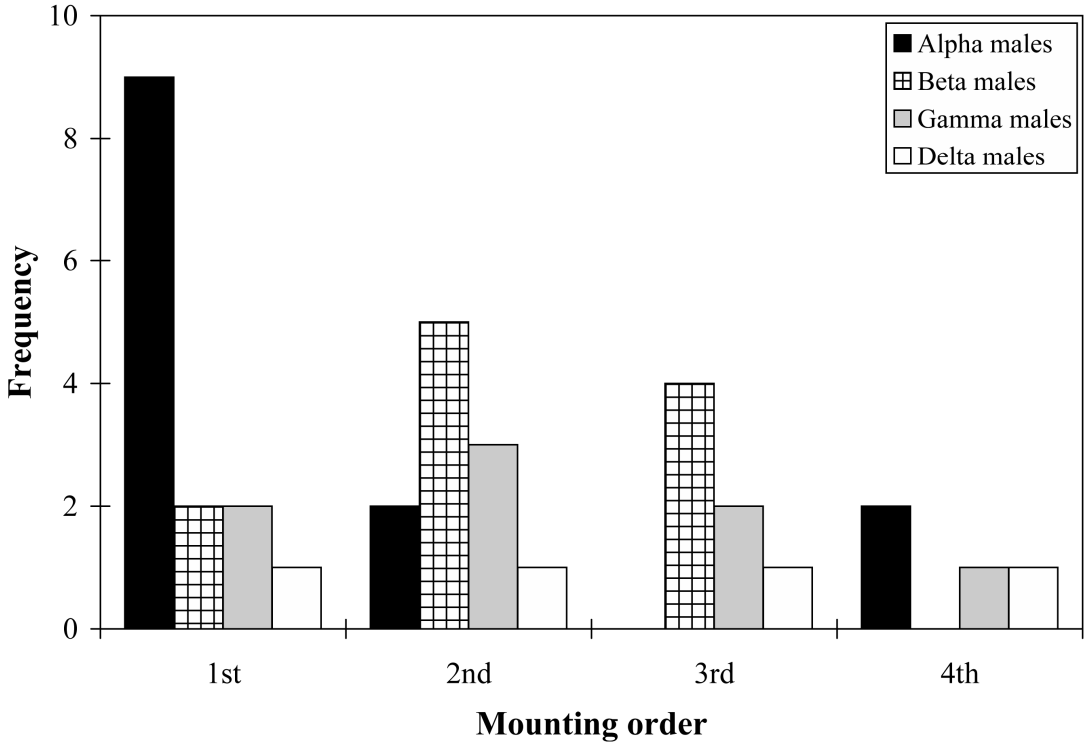

Figure 2.11: Mounting order by males of different dominance ranks. There was a significant positive correlation between male dominance rank and mount order, with males tending to mount in the order of their rank (Spearman rank correlation: $r_S = 0.345$, $n = 36$, $p = 0.04$).

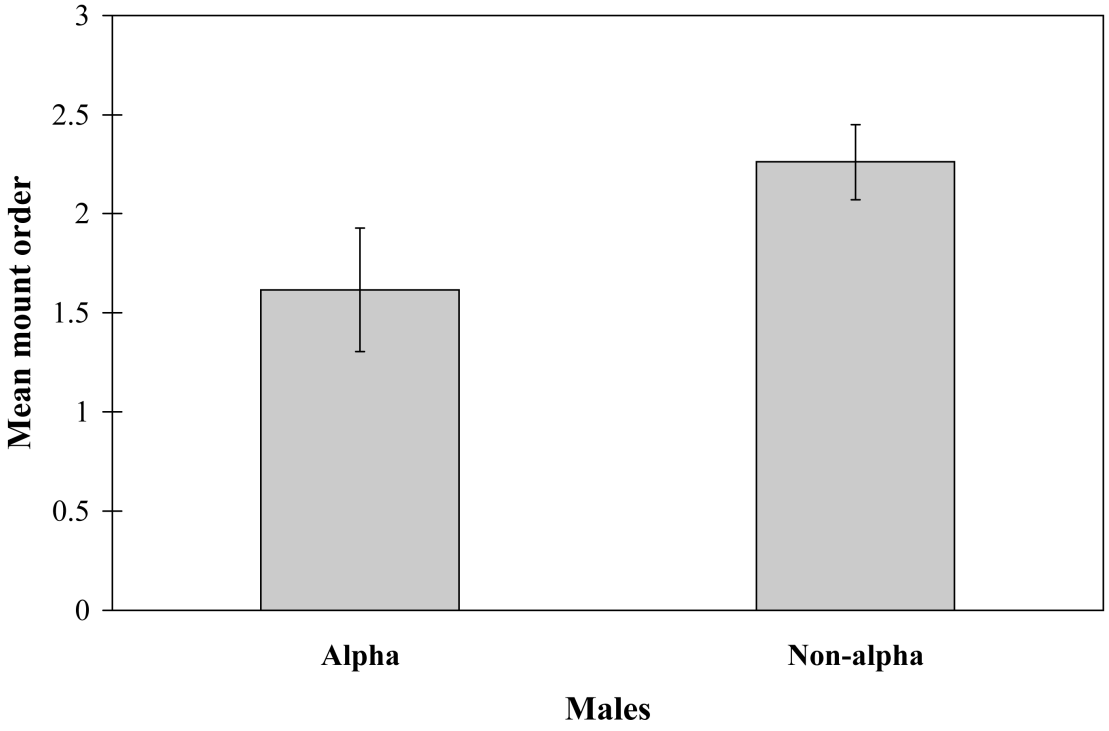

Figure 2.12: Mount order of alpha males versus males of all other dominance ranks. Mount order of alpha males occurred significantly earlier than non-alpha males in the mating queue (Mann-Whitney: $n_1 = 13$, $n_2 = 23$, $U = 85.5$, $p = 0.034$).

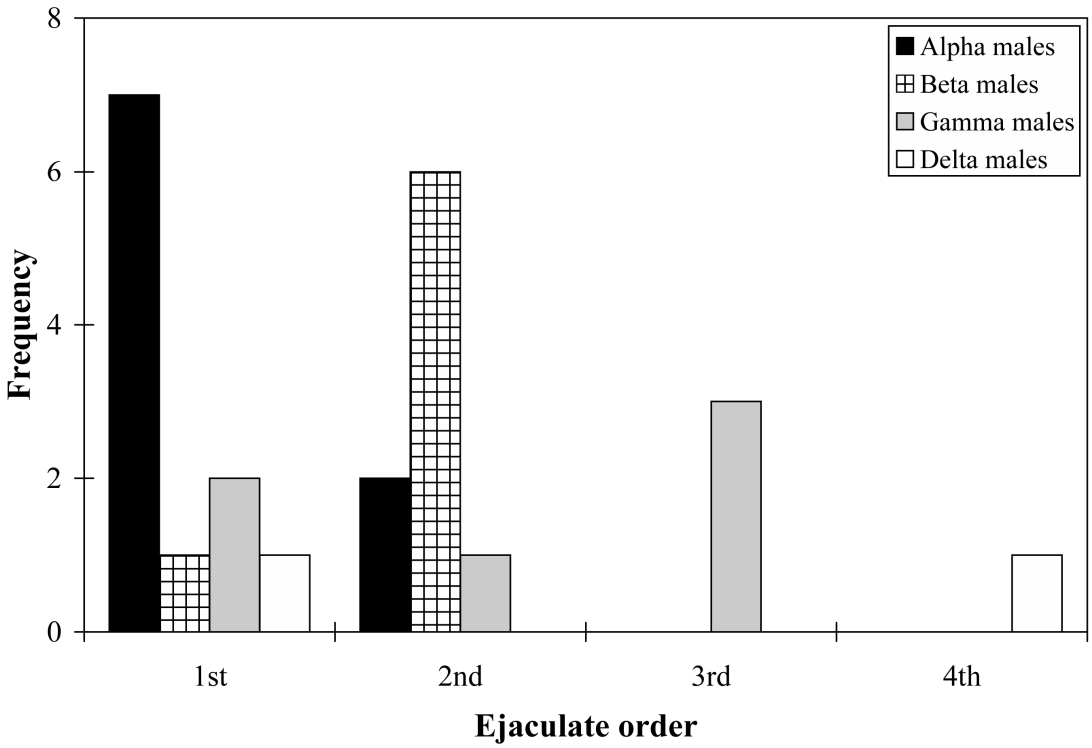

Figure 2.13: Ejaculate order by males of different dominance ranks. Males tended to ejaculate in the order of their dominance rank (Spearman rank correlation: $r_S = 0.479$, n =24, p = 0.018).

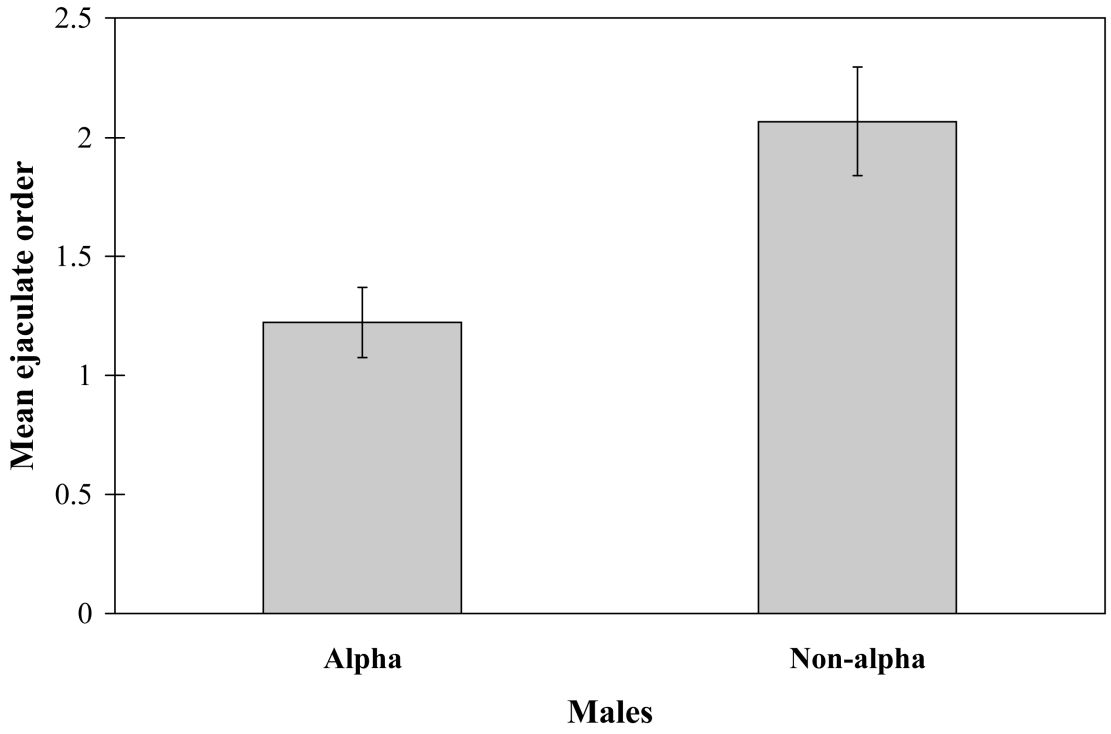

Figure 2.14: Ejaculate order of alpha males versus males of all other dominance ranks. Ejaculate order of alpha males occurred significantly earlier than for non-alpha males (Mann-Whitney: $n_1 = 9$, $n_2 = 15$, $U = 29.0$, $p = 0.021$).

CHAPTER 3: DOMINANCE RANK REVERSAL AS A MALE MATING STRATEGY

INTRODUCTION

Dominance Relationships: Predictability and Stability

Schjelderup-Ebbe (1922) was the first to introduce the concept of dominance relationships among animals by describing pecking order among domestic chickens. The subject of dominance relationships among animals has since received much attention among researchers, especially those studying non-human primate social behavior (Rowell, 1974; Bernstein, 1976, 1981; Popp and De Vore, 1979; de Waal, 1989; Lewis, 2002). Though many definitions and descriptions of the dominance concept have been suggested, one generally agreed upon characteristic of a dominance relationship between two individuals is predictability (Bernstein, 1981). Indeed, many primates show such stability in dominance relationships that dominance hierarchies often can remain consistent over long periods of time (i.e., cercopithecines: Walters and Seyfarth, 1987).

Because dominance is generally regarded as conferring priority of access to resources (Clutton-Brock and Harvey, 1976), models of male mating success frequently predict that only the most dominant male(s) will copulate as a result of their superior monopolization potential (Altmann, 1962). The implicit assumption in such models is that established dominance relationships among males will be upheld throughout mating periods. In some primates, male dominance relationships remain stable in mating

contexts, as in capuchin monkeys (*Cebus apella*), where alpha males are not interrupted by subordinate males while copulating (Janson, 1984; Lynch, 2001).

In contrast, male dominance relationships do not always remain stable throughout periods of mating in other primate species. For example, in the ringtailed lemur (*Lemur catta*), male dominance relationships can remain consistent in the months preceding the breeding season, but can become unstable during the mating season when intense and injurious male-male aggressive competition occurs (Jolly, 1966, 1967; Budnitz and Dainis, 1975; Taylor, 1986; Koyama, 1988; Sauther, 1991; Gould, 1994, 1997; Pereira and Weiss, 1991; Pereira and Kappeler, 1997; Sauther et al., 1999; Parga, 2002a, 2002b; Gould et al., 2005; Parga, 2006). Some researchers describe changes in male dominance relationships during mating periods as a general "breakdown" of the male dominance hierarchy (Jolly, 1967; Budnitz and Dainis, 1975; Sauther, 1991). This disruption of *L. catta* male dominance relationships (and its potential causes and consequences) is the subject of the present chapter. Before launching into a discussion of the particular aims of this portion of the study, however, general background information on *L. catta* social and reproductive behavior will be reviewed.

Background: Social and Mating Dynamics in *Lemur catta*

L. catta live in multi-male, multi-female groups in which both males and females have been observed to mate with multiple individuals of the opposite sex (Jolly, 1966, 1967; Sussman, 1974, 1991; Budnitz and Dainis, 1975; Mertl-Milhollen et al., 1979; Jolly et al., 1982b; Taylor, 1986; Koyama, 1988; Pereira and Weiss, 1991; Sauther, 1991;

Gould, 1994, 1996; Gould et al., 2003). Although females dominate males in this species, males within the same social group can show stable, well-defined dominance relationships with one another outside of the breeding season (Jolly, 1966, 1967, 1984; Budnitz and Dainis, 1975; Taylor and Sussman, 1985; Taylor, 1986; Kappeler, 1990a, 1993a; Pereira et al., 1990; Sauther, 1992, 1993; Gould, 1994; Nakamichi and Koyama, 1997; Pereira and Kappeler, 1997; Sauther et al., 1999).

Like most Malagasy primates, *L. catta* breed seasonally (Jolly, 1984; Rasmussen, 1985). Because females are only sexually receptive during the peri-ovulatory period (also known as vaginal estrus: Evans and Goy, 1968; Van Horn and Resko, 1977), all copulations are potentially conceptive. A single copulatory event can contain several separate mounts (some with and without intromission) before ejaculation is achieved, and males only ejaculate once with a female during a single estrus cycle (Sauther, 1991; Parga, 2003). *L. catta* can therefore be placed in category #10 (no copulatory lock, thrusting, multiple intromissions, single ejaculation) according to the schema devised by Dewsbury (1972) to describe mammalian mating patterns. Each female's estrus period lasts for approximately a day or less (Jolly, 1966; Evans and Goy 1968; Van Horn and Resko 1977; Koyama, 1988; Sauther, 1991). Some estrus periods can be as short as three and a half hours (Koyama, 1988; Sauther, 1991; Parga, 2006). Females in a social group will cycle within one to three weeks of one another (Sauther, 1991), and female *L. catta* can cycle up to three times per season if kept under natural light conditions, with each cycle being separated by an average of 39 days (Evans and Goy, 1968). Females almost always experience asynchronous estrus (Pereira, 1991; Sauther, 1991).

During the breeding season, *L. catta* males do not form cooperative coalitions with other males to increase their success in male-male competition, as occurs in some primates (e.g., chimpanzees, *Pan troglodytes*: Watts, 1998). Instead, male-male aggression over access to estrus females occurs between male dyads (Jolly, 1966; Koyama, 1988; Sauther, 1991). Both high- and low-ranking males copulate with females during the mating season, which has been found both in the present study (Parga, this work: Chapters 2, 5 & 6) and by others (Koyama, 1988; Pereira and Weiss, 1991; Sauther, 1991; Gould, 1994). Though males of all ranks mate with females, higher-ranking males tend to copulate earlier in the mating queue than lower-status males (Parga, this work, Chapter 2; Sauther, 1991).

This Study: An Analysis of Male Dominance Rank Reversals

The purpose of the present study was to provide a quantitative analysis of the frequency and types of male dominance status changes (rank reversals) during *L. catta* breeding periods. Several variables were tested as correlates and possible causal factors of male dominance rank reversals during periods of mating, and possible adaptive explanations for male dominance rank changes are considered. Male dominance rank reversal as a male mating strategy was also evaluated in the context of sexual selection theory.

METHODS

Study Site and Study Animals

The present study was conducted with four *L. catta* social groups on St. Catherines Island, GA, USA across a five-year period (Table 2.1). Provisioned, free-ranging *L. catta* groups have been maintained on St. Catherines Island (Thomas et al., 1978; Thomas, 1988) by the Wildlife Conservation Society since 1985 (Keith-Lucas et al., 1999). This site (located at 31º 40' N latitude, 80º 41' W longitude) is a privately-owned, largely undeveloped semi-tropical barrier island measuring 2,900 hectares, with a mixture of habitats, including pine, oak and palmetto forests, and open pastures as well as savanna and marsh (Keith-Lucas et al., 1999).

Keith-Lucas et al. (1999) provide a brief history of the *L. catta* colony on St. Catherines Island, including a description of lemur behavior following the initial release of six founder individuals. The lemurs on St. Catherines are provisioned daily with food (a mixture of monkey chow and fruits and/or vegetables), and water. The lemurs also forage on naturally-occurring vegetation, show ranging behaviors, and have established home range areas (Dierenfeld and McCann, 1999; Keith-Lucas et al., 1999). All adult lemurs have been fitted with uniquely-colored Telonics radio collars (Mesa, AZ). Subadults and small adults were often fitted with nylon collars. Differences in physical characteristics and shaving patterns were used to identify uncollared animals.

At one time, the *L. catta* colony on St. Catherines grew to over 75 individuals in four free-ranging groups (Parga and Lessnau, 2005). Each of these groups was studied across the duration of this project, though different groups were studied in each year.

Table 2.1 shows the groups that were studied during the start and middle of the breeding season in each year of this project (spanning late October-December). Table 2.2 shows the composition of each study group in early October (just prior to the start of the mating season) of each year. Each lemur group had between 5-11 females one year of age or older, and 2-4 non-natal males one year of age or older (Table 2.2).

Data Collection on Mating and Social Behavior

A. Breeding Season

Due to photoperiodic regulation, reproduction among *L. catta* on St. Catherines is approximately six months out-of-phase with the timing of these events in Madagascar, the endemic habitat of *L. catta* (Rasmussen, 1985). Mating behavior is limited to the fall and winter months (September-February) in the northern hemisphere if the lemurs are exposed to natural light (Evans and Goy, 1968; Van Horn, 1975). Data on mating behavior were collected during five consecutive breeding seasons: October-December 2000-2004, with additional data collected on mating behavior late in the breeding season of one year, during January-February 2004.

During breeding periods, data were collected daily from "dawn to dusk" using 'all-occurrences' sampling (Altmann, 1974) of agonism and reproductive behavior. In mating contexts, the following behaviors were recorded (in addition to recording the agonistic behaviors listed in section "B. Non-Breeding Season" below): jump-fights, mounts, thrusting, and female sexual presents. If observable, penile intromission, ejaculation, and copulatory plug displacement (Parga, 2003) were also recorded, though

observation conditions did not always allow these more detailed sexual behaviors to be verified. Ejaculation was indicated by the presence of semen in the female's peri-vaginal area, and/or on the tip of the male's penis. The start time (and stop time, if appropriate) of each behavior was recorded in seconds. Behavioral estrus was indicated by proceptive (sexual solicitation) or receptive (allowance of male mounting) behavior (Beach, 1976).

During the 2001 through 2004 breeding seasons, one to two field assistants helped monitor groups for estrus behavior and collect social and reproductive data. One observer was stationed per group unless a female was in estrus in one of the groups, in which case two observers paired up at the group with the estrus female.

B. Non-Breeding Season

During the pre-breeding months of each year (June-September in 2000 and 2004, and September-October 2001–2003), data were collected on social behavior approximately five days per week between the hours of 0600 and 1900, with the majority of samples collected between 0800 and 1600. Information on dominance relationships among males was gathered during this time via two main sampling techniques: continuous-time focal animal sampling, and 'all-occurrences' sampling for agonism (Altmann, 1974). Each sampling technique was performed separately, alternating between the two sampling types throughout the day. Each type of sample lasted for 20 minutes during 2000-2001, and was thereafter shortened to 15 minutes in duration. Focal sampling order was randomized, with no more than two samples per individual per day.

During focal samples, the following 'state' behaviors (Martin and Bateson, 1986) were recorded to the nearest second: rest, travel, feed, auto-groom, and allo-groom. The following 'event' behaviors (Martin and Bateson, 1986) were scored: approach, defecate, urinate, scent-mark (ano-genital, palmar, shoulder, tail), approach-withdraw, bite, chase, cuff, fight, grapple, lunge, nose-push, push, stink-fight, and take food (Jolly, 1966; Petter and Charles-Dominique, 1979; Taylor, 1986; Gould, 1994; Pereira and Kappeler, 1997; Parga, 2002a). *Ad libitum* data were collected at all times during all seasons of the year in both non-mating and mating periods to record sporadic or infrequent events such as predation attempts on the lemurs, instances of mobbing, and alarm or howling vocalizations.

Definition of Rank Reversal and Mating

A dominance rank reversal was defined as a change in the outcome of agonistic interactions between a male-male dyad as compared to the pre-breeding season dominance relationship existing between the dyad. Mating was defined as a male mounting a female. A more detailed definition such as 'mounting with penile intromission' or 'mounting with ejaculation' was not used because observation conditions did not always permit documentation of penile intromission or ejaculation during mounts.

Data Analysis

Discussions of dominance throughout this work refer to dominance expressed as the outcome of agonistic interactions (de Waal, 1989). All "decided" agonistic

interactions (Hausfater, 1975; Pereira and Kappeler, 1997) between males were used to construct the male dominance hierarchy within each group during the pre-breeding period of each year. Although dominance relationships among male *L. catta* are not always linear (Nakamichi and Koyama, 1997; Gould, 1994; Pereira and Kappeler, 1997; Sauther et al., 1999), male dominance relationships within each group in the years of this study were indeed transitive, enabling the use of a ranking system among group males. Agonistic outcomes between males during the pre-breeding period of each year were tallied in a matrix, as described in Bramblett (1994). This method allowed for a net dominance score to be calculated for each individual and a corresponding rank to be assigned to each based upon their relative dominance score.

To document male dominance rank reversals, the outcomes of dyadic male-male contests during periods of female estrus were analyzed. The frequency of male agonistic wins and losses were compared on days of estrus. The duration of all dyadic dominance rank reversals were calculated where possible (i.e., where the start of the reversal and end were directly observed). The start time of the rank reversal was considered to be the first instance of an agonistic win by the male who was lower-ranked during the pre-breeding season period. The reversal's end time was considered as the reversion to agonistic outcomes consistent with pre-breeding season male dominance rankings.

Only data from social groups in which a clear male dominance hierarchy existed during the pre-breeding season of each year were used in analyses. Two groups in two study years were identified as not having a discernable hierarchy: Group 1 in 2000, and Group 4 in 2004. Both were groups in which three of the four adult non-natal males

present in the group were recent immigrants. In 2000, WCS personnel released three novel unrelated males into Group 1 just prior to the start of the breeding season in September. Male dominance relationships were too variable in the short period of time prior to mating to identify a hierarchy. In the spring of 2004, three males immigrated of their own accord into Group 4. Too few agonistic interactions between the immigrants and the resident male of the group (DA, Table 2.2) were recorded to determine a male dominance hierarchy.

Analyses were performed using non-parametric statistics, including the Binomial test, Friedman's two-way ANOVA, Kruskal-Wallis one-way ANOVA, Mann-Whitney *U*, and Spearman rank correlation. All tests were two-tailed, and the significance level was set at 0.05. All means are reported with the standard error of the mean (SEM). Statistical tests were performed using Statistica, version 5.5.

RESULTS

A total of 40 estrus periods were observed in which females mated with at least one male. Of these estrus periods, 30 were in groups with discernable male dominance hierarchies (Table 2.3). Rank changes between males occurred during the estrus periods of 20 females in groups which had clearly-established male dominance hierarchies during the pre-breeding season. Full reversal of (or instability in) the dominance relationship of 53 male dyads were documented during these estrus periods (Table 3.1).

First Type of Male Dominance Rank Change: Clearly-Delineated Rank Reversals

Rank changes observed among males during mating periods could be categorized into three main types. The first type of male dominance rank reversal was very clear and well-defined. These reversals, termed "type 1" rank reversals in this work, consisted of a single, swift switch in the dominance relationship of two males, after which agonistic interactions were won consistently by the male who temporarily ascended in rank. These "type 1" rank reversals subsisted for a time until the dominance relationship between the two males reverted to pre-breeding season conditions in a second rapid dominance change-over.

Figure 3.1 represents a typical instance of a "type 1" rank reversal between two male *L. catta* during estrus. This rank reversal occurred during the estrus period of female JO in Group 2 in 2002 (Tables 2.3 & 3.1). As can be seen, there is a single rapid change in the outcome of agonistic interactions between the two males, and the previously lower-ranking gamma male, RY, won several interactions over the higher-ranking beta male of the group, BR, for a distinct period of time. This rank reversal lasted for just under 25 minutes. Note that following several agonistic wins by the previously lower-ranking male (wins which constitute this male's rank reversal), the males' agonistic relationship reverted to pre-breeding season conditions. Clearly-delineated temporary reversals such as that shown in Figure 3.1 were witnessed on 25 different occasions (Table 3.1). These well-defined rank reversals of known duration lasted anywhere between a few minutes to a few hours (Table 3.1). Among "type 1" rank reversals of known length, the mean (±SEM) duration of reversals was 64±13 minutes.

Clearly-delineated rank reversals were almost always shorter in duration than the female's full estrus period.

Similarly, Figure 3.2 shows another "type 1" rank reversal between two male *L. catta*. This rank reversal occurred during the estrus period of female RR in Group 3 during 2001 (Tables 2.3 & 3.1). In Figure 3.2, the group's delta male, MC, reversed rank temporarily over the group's beta male, KL. Again, the rank reversal constituted a clear departure from the pre-breeding season dominance relationship of these two males (Table 2.3). This rank reversal lasted longer (70 minutes) than the rank reversal depicted in Figure 3.1, but both reversals resemble one another with respect to the consistency of agonistic wins by a previously lower-ranking male following the initial swift reversal. Also, in both cases, the reversal ends with a single agonistic interaction marking the switch back to pre-breeding season dominance relations between the male dyad.

Second Type of Male Dominance Rank Change: Agonism with Variable Outcomes

The second type of rank change observed between male *L. catta* consisted of extremely frequent agonistic interactions between two males in which the outcome was neither predictable nor consistent (i.e., either of the males could 'win' then 'lose' agonistic interactions in quick succession). Figure 3.3 portrays this second type of rank reversal ("type 2"). The example shown in Figure 3.3 occurred during 2003 in Group 2 between the group's delta male, LE, and the group's beta male, ED, during female TO's estrus period (Tables 2.3 & 3.1). The "type 2" rank reversal shown in Figure 3.3 lasted for a total of 2 hours and 23 minutes. Notice that the major difference between this type

of male dominance rank reversal and the "type 1" previously portrayed is the lack of consistency in the outcome of successive instances of male-male agonism. Whereas "type 1" reversals showed a single clear switch in dominance between a male-male dyad which persisted for a period of time, in "type 2" rank reversals, dominance relationships appeared to be in near-constant flux throughout the reversal.

Figure 3.4 shows another example of this second form of male dominance rank reversal. This period of rank instability lasted for 2 hours and 28 minutes. This "type 2" rank reversal occurred during the estrus period of female KA in Group 2 between the group's gamma male, RY, and the group's beta male, ED (Tables 2.3 & 3.1). Though the female was in estrus across several hours of the day, this period of rank instability occurred during only one portion of her estrus period. Again, as in Figure 3.3, there is much instability in the dominance relationship between these two males, which is exemplified by the variability in the outcome of successive agonistic interactions.

For "type 2" reversals of known duration, the mean (±SEM) was 144±35 minutes, though "type 2" reversals lasted between 19 minutes and approximately six and a half hours. "Type 2" rank reversals occurred in 25 male dyads across the course of this study, and all were characterized by frequent changes in the outcome of male-male agonism. Hence, clearly-defined rank reversals ("type 1") and dominance rank reversals with greater instability ("type 2") occurred with equal frequency in the present study (Table 3.1).

Third Type of Male Dominance Rank Change: Single Win by a Lower-Ranked Male

In three instances, there was a single agonistic interaction won by the previously lower-ranking male over a more dominant male during a female's estrus period. In each of these instances, following the lower-ranking male's single win, all subsequent agonistic interactions were once again won by the higher-ranking male (upholding the pre-breeding season dominance relationship between the two males). Figure 3.5 shows an example of this third type of male dominance rank change, which occurred in 2001 during the estrus period of female MA in Group 3 (Tables 2.3 & 3.1). Male KL, the alpha male of the group, was defeated once during this female's estrus period by the group's beta male, MN. A third classification was warranted because a single agonistic interaction won by a lower-ranking male constitutes neither a clearly-defined dominance rank reversal ("type 1") nor a situation in which male-male agonistic outcomes are highly variable ("type 2").

What Determined the Type of Male Dominance Rank Change During Estrus?

It was of interest to investigate possible predictors of each type of male dominance rank change during the breeding period. Because the majority of dominance rank changes among male dyads took the forms of either "type 1" or "type 2" dominance rank changes, the following analyses focused solely on these two main types of rank reversals. In short, an attempt was made to answer the following question: During a single estrus period, why do some male dyads show a single clearly-defined dominance

rank reversal ("type 1"), whereas others show much more instability and several changes in dominance ("type 2")?

One possibility was that the level of instability in the dominance relationship between two males may have been due to differences in age. One expectation might be that males who are closer in age would be physically more closely-matched in male-male competition, and therefore would exhibit more agonistic instability ("type 2" rank reversals). To investigate this possibility, the absolute value of the age difference between the male dyad members was calculated, and compared based upon whether their documented rank change was of the "type 1" or "type 2" form.

The age difference between males did not predict the type of dominance rank reversal between them during estrus (Mann-Whitney: $n_1 = 25$, $n_2 = 25$, $U = 282.5$, $p = 0.564$, NS). Male ages can be found in Table 2.2. A separate analysis was performed to test whether the age of the male performing the rank reversal (and ascending in rank) determined the type of dominance rank change between he and a higher-ranked male. The age of the male performing the rank reversal was also a poor predictor of the form of the rank reversal (Mann-Whitney: $n_1 = 25$, $n_2 = 25$, $U = 250.0$, $p = 0.231$, NS). The age of the male who temporarily lost agonistically to a previously lower-ranked male was also a poor predictor of the type of rank reversal (Mann-Whitney: $n_1 = 25$, $n_2 = 25$, $U = 295.0$, $p = 0.744$, NS).

Another route of investigation concerned pre-breeding season male dominance rankings, and whether this variable could predict the type of dominance rank change between two males that occurred during an estrus period. The rank reversing male's pre-

breeding dominance rank did not show a significant relationship with whether the dominance rank change was of the "type 1" or "type 2" form (Mann-Whitney: $n_1 = 25$, $n_2 = 25$, $U = 234.5$, $p = 0.131$, NS; Table 3.1). Neither did the dominance rank of the male temporarily "losing" rank predict what form the rank reversal would take (Mann-Whitney: $n_1 = 25$, $n_2 = 25$, $U = 269.5$, $p = 0.407$, NS; Table 3.1). The number of ranks separating the two males was also tested to see whether it could predict the form that their rank reversal would take during the mating period. However, the distance in rank between two males also did not predict the type of rank reversal observed between them (Mann-Whitney: $n_1 = 25$, $n_2 = 25$, $U = 291.0$, $p = 0.686$).

The last variable considered as a potential factor influencing the form of dominance rank reversal was whether or not the male dyad was composed of individuals who were familiar with one another (Table 3.1). Presumably, males who spent a previous mating season in the same group would have greater familiarity with (and knowledge about) one another. One expectation might be that pairs of males with less knowledge of an adversary's fighting ability might show greater dominance instability during periods of mating competition. Hence, one might expect more "type 2" dominance rank reversals among males who did not spend the previous breeding season in the same group. Though not significant (Friedman's 2-way ANOVA: $\chi^2 = 0.33$, df = 1, $p < 0.564$, NS), there were indeed more "type 2" reversals among males who did not spend the previous breeding season together (Figure 3.6).

Effect of Female Sexual Behavior on Male Rank Changes

Among rank reversals for which the start time was known (n = 50), 70% of reversals began following either: 1) the female's allowance of mounting by the lower-ranked male, and/or 2) a sexual present by the estrus female to the lower-ranked male. Female proceptive or receptive behavior to the lower-status ('rank reversing') male preceded rank reversals more frequently than would be expected by chance (Binomial test, $p = 0.002$).

For each male-male dyad in which a rank reversal was preceded by female proceptivity and/or receptivity to the lower-status ('rank reversing') male, the time between the rank reversal and the female's first present (or allowance of mounting) to the lower-status male was calculated. The median time from a female's first demonstration of sexual preference to a lower-ranking male (in the form of a present or allowance of mounting) to the start time of a rank reversal by that male was 47 minutes across all dyads for which this duration was known (n = 36). The mean time was 87.3±17 minutes, though rank reversals occurred between 14 seconds and 340 minutes following a male's receipt of proceptive or receptive behavior. Because some males contributed more than one data point to the above analyses (as they reversed rank more than once), a single averaged value per male was calculated. These results show that the mean duration between female proceptive and/or receptive behavior directed towards a lower-ranking male and his subsequent reversal was 82±23 minutes (n = 10).

Out of 36 cases in which this duration was known, in 20 instances (56%), the lower-ranking male won his first interaction within one hour of receiving proceptive or

receptive behavior from the estrus female. In 16 out of 36 cases (44%), lower-ranked males reversed rank within 30 minutes of receiving proceptive or receptive behavior by the female. Nine out of 36 males (25%) reversed rank within 10 minutes or less of receiving proceptive or receptive behavior by the estrus female. Considering the multi-hour estrus duration of many females (refer to Figures 3.1-3.5), these data show that there is a remarkable temporal coupling between female exhibition of sexual preference towards a male (in the form of proceptive and receptive behavior) and subsequent rank reversal behavior by the sexually preferred male.

Additionally, across all rank reversals for which the duration was known, there was a strong positive correlation between males' pre-breeding season dominance rankings, and the amount of time between the first receipt of receptivity or proceptivity and the start of their rank reversal (Spearman rank correlation: $r_S = 0.395$, $n = 36$, $p = 0.017$). So as not to bias this analysis by including several data points from the same male, in separate analyses comparing the time duration from the first exhibition of female proceptivity and/or receptivity to a male and that male's subsequent reversal, each male only contributed a single data point (representing their mean) within each dominance rank category. Only male MN (Table 3.1) contributed a point to more than one rank, beta and gamma. Figure 3.7 shows that male pre-breeding season dominance rank tends to have an effect on the speed with which males performed rank reversals, with lower-ranking males taking longer to reverse rank, but this trend does not reach statistical significance (Kruskal-Wallis one-way ANOVA: $\chi^2 = 4.32$, $df = 2$, $p < 0.116$, NS).

Effect of Ejaculation on Male Rank Changes

The majority of males reversing rank did not revert to their pre-breeding season ranking until after they ejaculated with the estrus female. In 70% of instances in which it was known whether the rank reversing male ejaculated at the end of a rank reversal (n = 27), males ejaculated with the estrus female before their rank status returned to pre-breeding season conditions. In fact, males ejaculated before the end of their rank reversal more frequently than would be expected by chance (Binomial test, $p = 0.017$). The mean time from a rank reversing male's ejaculation to the end of his reversal ranged between 10 seconds to 84 minutes, with a mean time of 33.1±6.5 minutes (n = 8 different males). Each male who performed more than one rank reversal had his values averaged so that each male contributed only a single data point to the calculation of the mean. Notably, in 82% of reversals in which this duration was known (n = 17), a male's rank reversal ended within an hour of his ejaculation.

For comparison, the speed with which higher-ranked males *lost* rank following ejaculation (marking the beginning of another male's rank reversal over them) was also calculated. A single mean value for this measure was calculated for all higher-ranked males who experienced a reversal, so that each male contributed only a single data point to the calculation of the mean. Results show that higher-ranking males who began losing agonistic interactions following their ejaculation did so between 5 and 105 minutes following their ejaculation, with a mean time of 24.9±9.8 minutes (n = 5 different males). In 90% of reversals in which this duration was known (n = 10), higher-ranked males began to lose agonistically due to a subordinate male's rank reversal within an hour of

their ejaculation. Clearly, loss of dominance (by both higher-ranked males and the males who reverse rank over them) occurs fairly rapidly following ejaculation.

DISCUSSION

Dominance Rank Changes Among Male *L. catta* During Mating Periods

As this study has demonstrated, changes in male-male dominance relationships are extremely common during *L. catta* mating periods. Indeed, several previous studies have noted that changes in dominance relationships can occur during the breeding season among *L. catta* males (Jolly, 1966, 1967; Budnitz and Dainis, 1975; Taylor, 1986; Koyama, 1988; Sauther, 1991; Pereira and Weiss, 1991; Gould, 1994, 1997; Pereira and Kappeler, 1997; Cavigelli and Pereira, 2000). However, none of these studies has presented quantitative data on the frequency or duration of these male rank reversals, as was done in the present chapter. The present study also identifies female sexual behavior (proceptivity and receptivity) and ejaculation as key factors affecting dominance rank reversals among male *L. catta*.

The first form male dominance rank changes took during the mating period was that of clearly-delineated male rank reversals in which the dominance relationship between two males reversed as a result of a successful challenge by a subordinate that lead to an agonistic 'win' for that male. These "type 1" rank reversals typically lasted between a few minutes to a few hours in duration, after which the males' dominance ranks reverted back to pre-breeding status, as indicated by the direction of agonistic wins.

In “type 2” male dominance rank reversals, the outcome of male-male agonistic interactions were highly variable, and were neither consistent nor predictable. In “type 2” reversals, dominance relationships could change between two males several times within just a few hours’ time. These reversals were markedly different than the “type 1” clearly-delineated rank reversals which lasted for a period of time then reverted back to pre-breeding season conditions. In contrast, “type 2” reversals were characterized by their unpredictability, and many were typically longer than “type 1” reversals (Table 3.1). Some “type 2” reversals lasted for several hours during a female’s estrus period. Both types of male dominance changes (clearly-delineated “type 1” reversals and highly variable outcome “type 2” reversals) were documented with equal frequency during this study.

A third form of dominance rank reversal among males consisted of a single agonistic win by a previously subordinate male, before and after which the pre-breeding season male dominance relationships were upheld. “Type 3” rank reversals were relatively uncommon, occurring only on three occasions during the study. Though it was heuristically useful to describe each of the three distinct types of dominance rank changes documented in this study, it is important to note that the disruption of pre-breeding season dominance relationships between males is a common element to all forms of reversal. The fact that some of the same males reversed rank over higher-ranking male group members more than once during the same mating season further illustrates the degree to which male dominance relations are in flux during the socially tumultuous *L. catta* breeding season.

One obvious question was why some male dominance rank reversals occurred in a clearly-delineated fashion, whereas others showed highly variable agonistic wins among males. One expectation was that males who were more closely matched with respect to age or dominance status would have more highly variable outcomes during male-male competition. Somewhat surprisingly, the age difference between males (and the difference in their pre-breeding season dominance statuses) did not seem to affect the form that the dominance hierarchy disruption took (i.e., whether the outcome of male-male competition was highly variable or consistent for a period of time following the initial reversal). Males were no more or less likely to have agonistic interactions with highly variable outcomes if there were more years or dominance ranks separating them. Likewise, the age and pre-breeding season dominance ranks of the males performing the reversals (and that of the higher-ranking males losing to such males) were tested as possible predictors of rank reversal type, but none of these variables showed a significant relationship with the form a rank reversal took between a male-male dyad.

The last line of inquiry into potential variables affecting the form of rank reversals was the familiarity of the males involved. As noted by Clutton-Brock and Harvey (1976), rank reversals among male primates may occur when combatants cannot judge the outcome of the aggressive interaction, either because the males are unfamiliar with one another, or because they do not have prior information on the fighting ability of other group males. It was therefore expected that males who had not spent an entire breeding season engaging in male-male competition with their rival (or at the very least, observing their rival engage in competition with other males) would perhaps have more trouble

gauging the fighting ability of their opponent, resulting in more variable agonistic outcomes when the two did come into agonistic conflict. Results showed that there were indeed more "type 2" rank reversals (indicating more dominance instability) among males who had not spent the previous mating season in the same group, though this trend was not statistically significant. At present, there is no strong predictor of the form a dominance rank reversal will take between two male *L. catta*.

Influence of Female Mate Choice and Ejaculation on Male Dominance Rank Reversals

Two factors were tested for their influence on male rank reversal behavior: female exhibition of sexual preference, and ejaculation. The effects of both factors will be discussed in turn. Presumably, being the receiver of female proceptive or receptive behavior might influence a lower-ranking male's decision about the amount of agonistic effort to exert against a higher-ranked male during mating competition. Similarly, because male *L. catta* ejaculate only once with a female during a single estrus period (Sauther, 1991; Parga, 2003), the event of ejaculation is expected to influence the amount of effort a male allocates to male-male competition, because the female may be of lesser value to a male following his insemination of her.

In the majority of instances of rank reversal (70%), the lower-ranking male's first agonistic win was preceded by the estrus female's exhibition of proceptivity or receptivity to him. Hence, female mate choice behavior is a key factor which appears to positively influence the aggression of non-alpha males against higher-ranked males during estrus. Female *L. catta* sexual behavior directed towards non-alpha males might

even be described as "inciting" male-male competition, functioning similarly to the "protest" vocalizations of female elephant seals, *Mirounga angustirostris*, which ensure that male-male competition selects for superior males (Cox and Le Boeuf, 1977). Interestingly, it appears that males who were higher-ranking during the pre-breeding season were able to achieve rank reversals faster following their receipt of proceptivity or receptivity by the estrus female than were lower-ranking males, though this trend did not reach statistical significance.

Ejaculation was an event that appeared to influence rank reversals. The majority of males who reversed rank (for whom such information was known) ejaculated before their rank reversal ended. Males who ejaculated before the end of their rank reversal showed a fairly quick return to pre-breeding season conditions following their ejaculation; all such rank reversals ended within 90 minutes of the rank reversing male's ejaculation. Likewise, for higher-ranking males who lost rank to a rank reversing male, rank loss typically followed their ejaculation. The vast majority of these higher-ranking males (who lost rank due to a reversal) began to do so within one hour of their ejaculation. In sum, males tended to reverse rank following female sexual preference directed towards them, and ejaculation appeared to hasten the loss of rank by higher-ranking males who lost rank during reversals, and more subordinate males reversing rank.

Explanation for Dominance Rank Changes During Mating Periods

If high dominance status is an indicator of "good genes" (Andersson, 1994), it is questionable why alpha males do not consistently maintain their top-ranked status

throughout a single, temporally short estrus period. As suggested by Popp and DeVore (1979) in their seminal work on aggressive competition and social dominance, not every resource is of equal value at all times to an individual. Consequently, dominance hierarchies may be time- and resource-specific (Popp and DeVore, 1979; but see Lewis, 2002). Accordingly, even high-ranked males may decrease the effort they put towards male-male competition as the value of the contested resource (in this case, the estrus female) changes. For example, after a male has mated with a female, his projected payoff in reproductive units may be significantly less than earlier in the female's estrus period (i.e., before he mated to ejaculation). Perhaps further mating effort on his part would result in only incremental increases in his probability of fertilization success. Decreased resource value of the female may explain why males do not mate guard females continuously throughout their sexually receptive periods. This may explain why some males began "losing" agonistic interactions shortly following their insemination of an estrus female. If a female is already inseminated and an alpha male was her first mate (as frequently occurs: see Chapter 2), the additional gain from continued mate guarding behavior may not be worth the cost to the male in some cases. Throughout the hours of estrus, the mating status of the female changes (e.g., she is first uninseminated, then is inseminated once, then perhaps twice, and so on). Consequently, a male's chance of achieving fertilization may successively decline as estrus progresses due to increased levels of sperm competition (Parker, 1970). Decreased chances of fertility by later-mating males may be especially true if there is first-male sperm precedence in this species, as suggested by Pereira and Weiss (1991).

Another potential reason dominance changes occur among male *L. catta* during periods of estrus may be that males' resource holding potential (Parker, 1974) can decline across time if they become ill, injured, experience dehydration or become exhausted, because such physical changes can alter a male's ability to fight. Hence, both the projected gains of mating and the associated costs of male-male competition may be constantly changing for each male, and may be asymmetric between male competitors. This asymmetry in resource value and in the costs associated with fighting to attain the resource in question may explain why more subordinate *L. catta* males are willing to attempt male dominance rank reversals. The cost-benefit ratio for an as-of-yet unmated male may be considerably lower than for a male who has already ejaculated once with a female.

Another possibility is that dominance rank changes occur among males because of a difference in motivation (Lewis, 2002) between two males competing over mating access. If one male has mated and the other has not yet mated, the unmated male may have higher motivation to mate than does a male who has already inseminated the female. Motivation can be defined as an asymmetry in need (Lewis, 2002). In this scenario, though the resource value (an unfertilized egg) may be the same for both males, one male is more highly motivated to attain that resource, which may cause a dominance rank reversal.

Why Risk Injury or Death to Attempt a Rank Reversal?

Rank reversal appears to be a potentially risky strategy, because a male may incur serious injuries and mortal wounds as a result of engaging in escalated physical combat with a higher-ranking male competitor. One obvious question is why male *L. catta* would be willing to risk such injury and even death by challenging a more dominant male. Part of the explanation for this risky male behavior may be that for *L. catta* males, every opportunity to copulate with a female is extremely valuable due to its rarity. Females only mate during their day-long estrus period and will cycle at most three times per year (but only once if they conceive during their first estrus cycle), providing males with very few chances to inseminate a female (Jolly, 1966; Evans and Goy 1968; Van Horn and Resko 1977; Koyama, 1988; Sauther, 1991; Parga, 2006). Hence, time appears to be a crucial limiting factor for male *L. catta* reproductive success. Gaining access to an estrus female via rank reversal, though risky, may be worth the cost in potential reproductive units gained.

Also, sneak copulations may be difficult to achieve, and this may be an especially marked problem for *L. catta* males on St. Catherines Island. Dense vegetation is a characteristic of *L. catta* wild habitat (Sussman, 1974, 1977). In contrast, with some exceptions (i.e. dense thickets of saw palmetto), dense vegetation is largely absent on St. Catherines Island (Thomas et al., 1978). Therefore, just as observation conditions for researchers are favorable given the largely open habitat on St. Catherines, so too may the visibility of mating pairs be favorable for competitor males, which may decrease opportunities for sneak copulations. Hence, if opportunities for sneak copulations are

unlikely, the rank reversal strategy – potentially costly though it may be – may be the only dependable strategy by which a lower-ranking male can gain access to an estrus female.

Dominance Rank Reversals: A Comparison with Other Primates

A common description of dominance rank changes among male primates is that such changes take a long period of time to occur. For example, Riss and Goodall (1977) and de Waal (1982) describe changes in the male dominance hierarchy of chimpanzees (*Pan trogloydytes*), and note that status changes among males can take months to develop, during which time the dominance relationships between pairs of males can become difficult to discern. Similarly, Witt et al. (1981) documented a switch in dominance rank between an alpha and beta male in Barbary macaques (*Macaca sylvanus*) during the mating season which was preceded by an increasing number of agonistic interactions between the two males, which the authors interpreted as challenges by the lower-ranking male. Males are frequently described as maintaining their new dominance status for months or even years following a dominance rank reversal (Riss and Goodall, 1977; Witt et al., 1981; de Waal, 1982).

Gradual dominance rank changes among male *L. catta* do occur, and new ranks can sometimes be maintained long-term (Sauther et al., 1999), unlike the ephemeral rank changes which occur during mating periods described in this chapter. Often times, such male rank changes (which can be maintained for several months or more) occur during male migration periods (Gould, 1994). During the course of the present study, there were

indeed changes in male dominance rankings from one year to the next which could be maintained for several months, and sometimes for years (see Table 2.3).

However, the rank reversals described among *L. catta* males in this chapter are uniquely different, because they represent *temporary* shifts in dominance on days of female estrus. They are more akin to dominance rank changes that happen rapidly, such as dominance shifts among male mandrills, *Mandrillus sphinx*, which take one day to achieve (Setchell et al., 2005). Still, such descriptions are of situations in which males maintain their new dominance status for a substantial period of time following the dominance change. Among the *L. catta* males in this study, dominance rank reversals could last for just a few hours on days of estrus – indeed, in some cases, mere minutes – after which they reverted to pre-breeding season conditions.

There are two potential reasons to explain why male dominance rank reversals in *L. catta* appear to be so different from the male dominance status reversals observed in other primates. First, male *L. catta* do not form coalitions. Male coalitions can enable many anthropoid male primates to ascend and maintain dominance (chimpanzees, *Pan troglodytes*: Riss and Goodall, 1977; de Waal, 1982; Watts, 1998) or gain access to estrus females (e.g., olive baboons, *Papio cynocephalus anubis*: Packer, 1977; Smuts, 1985; Bercovitch, 1988; Noe and Sluijter, 1990; Noe, 1992). Instead, in *L. catta*, the male-male aggression that occurs during mating periods is between male dyads (Jolly, 1966; Koyama, 1988; Sauther, 1991). Though different pairings of male-male dyads aggressed against one another in the present study, two males were never observed joining forces against a third male simultaneously during a female's estrus period. Gould (2006) has

recently raised the possibility that male *L. catta* may form coalitions of a sort – for example, when they are transferring in pairs or triplets into a new social group during the male migration season. However, if these male associations are coalitions, they are very different than male coalitions that occur among anthropoids (Gould, 2006). One example of this difference is that male *L. catta* do not solicit agonistic aid from male affiliative associates as do male chimpanzees, *Pan troglodytes* (de Waal, 1982).

Another reason male dominance rank reversals in *L. catta* during mating periods are different from those in other primates is that such rank reversals are temporary. The unique ephemerality of male *L. catta* dominance rank changes during estrus may be due to the fact that individual females are sexually receptive for just a few hours to one day (Jolly, 1966; Sauther, 1991; Parga, 2006). If ascending in rank primarily functions to increase a male's mating success, maintaining a higher dominance status for a longer period of time than is necessary to inseminate a female would likely be costly. Maintenance of rank over a longer period of time may not increase a male's reproductive success beyond that which is gained by a short rank reversal. In contrast, females of many anthropoid primate species can be sexually receptive across a period of several weeks (Martin, 1992), making a short rank reversal in these species potentially unprofitable for males. Hence, if dominance is primarily useful for conferring priority of access to an estrus female (but if maintaining high dominance rank is costly), then male *L. catta* may not gain by ascending in dominance rank for longer periods of time (several weeks or months) than was observed in this study.

The question remains, though, of why a male does not reverse rank only once during the estrus period of the first female to cycle during the mating season, and then remain dominant throughout the next few weeks until all females have sexually cycled. One possibility is that maintaining high dominance status for even a two to three week period is too costly for *L. catta* males. Indeed, if pre-breeding season alpha males cannot hold onto their alpha position, lesser quality males can hardly be expected to ascend and maintain dominance throughout the mating season.

During periods of rank instability (which is what rank reversals of all three types may be considered), a striking element of a previously lower-ranking male's behavior is his adamant challenges to a higher-ranking male. *The main causal factor for rank reversals among L. catta males during periods of mating therefore appears to be the increased propensity of lower-ranking males to challenge the role of higher-ranking males.* This supports Rowell's (1974) contention that dominance hierarchies are primarily maintained through the subordinate behavior of lower-ranking individuals.

Dominance Rank Reversals in a Non-Primate Promiscuous Mammal

A similarity to the dominance rank reversals which occur among male *L. catta* described in this study occurs in the tassel-eared squirrel (*Sciurus aberti ferreus*) during mating periods. In this small mammalian species, males establish dominance relationships. However, some subordinate males (if they are able to circumvent the guarding tactics of more dominant males) become highly aggressive for a short time following their copulation with a female, and are able to defeat dominant males and

become temporarily dominant (Farentinos, 1972). Just as in the *L. catta* rank reversals described in this chapter, the male squirrels are able to temporarily win agonistic encounters over more dominant males, but they do not permanently maintain their ascension to dominance (Farentinos, 1972). The post-copulatory aggression exhibited by these previously-subordinate males may function as mate guarding, because a recently-inseminated female is most likely a valued resource for the male who completed the copulation. Farentinos (1972) suggests that the temporary increase in aggression exhibited by these subordinate male squirrels may be related to a physiological side-effect of contact with the female. Similarly, among *L. catta* in this study, female sexual behavior in the form of sexual presents and allowance of mounting to lower-ranked males appeared to stimulate these males to expend greater effort in male-male agonism. Hence, the unique agonistic dynamics observed among male *L. catta* during mating periods share similarities with another promiscuously-mating mammal which shows male-male contest competition over sexually receptive females.

CONCLUSIONS

This chapter provides quantitative evidence for rank changes among male *L. catta* during periods of mating. Every study group having a distinct male dominance hierarchy at the start of the breeding season showed rank changes among males during periods of estrus, making male rank reversals an exceedingly common event during mating periods. Male rank reversals took three distinct forms, all with differing levels of dominance instability among male-male dyads.

In the first type of dominance rank change, termed here "type 1," a single, swift switch in the dominance relationship between two males occurred, after which agonistic interactions were won consistently by the male who temporarily ascended in rank. "Type 2" rank reversals consisted of agonistic interactions between two males which showed highly variable outcomes. This type of reversal was characterized by much dominance instability between the two males throughout the duration of the rank reversal. In "type 3" rank reversals, a single agonistic interaction was won by the lower-ranking male over a more dominant male; before and after this agonistic win, all agonistic interactions were won by the higher-ranking male. "Type 1" and "type 2" rank reversals occurred with equal frequency during the study. "Type 3" dominance changes were more rare, and only occurred in three instances in the course of this multi-year project. At present, there is no clear predictor of the form a dominance rank reversal will take between two males.

Two factors appeared to markedly affect rank reversals: 1) the exhibition of female proceptivity and receptivity to a non-alpha male, and 2) ejaculation. The majority of rank reversals were preceded by female proceptive or receptive behavior to the lower-ranking male. It appears that this female sexual behavior may serve as a signal to the male of his projected payoff (e.g. sexual acceptance by the estrus female), making him more likely to attempt a rank reversal. Likewise, ejaculation by the rank reversing male was closely followed in many cases by the end of the rank reversal. For higher-ranked males as well, ejaculation appeared to be followed by the loss of dominance. For both categories of males (those who gained and lost rank during a reversal), agonistic loss following ejaculation may be a conservative strategy which enables them to cease

expending extra mating effort following their ejaculation. Agonistic loss following ejaculation may also be due to a somatic physiological response by the male (perhaps involving hormonal changes resulting from the ejaculation) which make him less able (or less willing) to continue engaging in the costly agonistic interactions required to maintain dominance.

The rank reversal strategy appears to be integrally important to the mating success of non-alpha *L. catta* males, because reversals provide mating opportunities to such males (Chapter 2). Unless they are able to agonistically dominate other males in the vicinity, males are forced to either sneak copulations or perform evasive copulations (Chapter 2). For a non-alpha male, rank reversals preclude the need for either of these alternatives strategies by enabling a male to agonistically dominate other males – at least for a short time – allowing him to gain access to and mate with the estrus female.

Most of the rank changes documented in this study were extremely short in duration, and lasted for a period of minutes or hours. These rank reversals occurred during estrus, and most ended before the cessation of the female's estrus period. Therefore, rank reversal appear to function as an efficient mating strategy in which males expend effort in male-male competition when it most counts – when a female is sexually receptive.

Table 3.1: List of all rank reversals occurring in groups having male dominance hierarchies during the pre-breeding season of each year

Year of Study	Group	Female	Male performing rank reversal	Higher-ranking male losing dominance	Type of rank reversal	Rank reversal duration (min)	Pre-breeding season rank of male performing reversal	Pre-breeding season rank of male losing rank during reversal
2000	3	LS	ED	BY	Type 1	Unknown	Beta	Alpha
		MA	ED	BY	Type 1	56.9	Beta	Alpha
		JN	ED	BY	Type 1	70.9	Beta	Alpha
2001	3	JA	MN	BY	Type 2	Unknown	Gamma	Alpha
		JA	KL	BY	Type 1	Unknown	Beta	Alpha
		MA	KL	BY	Type 2	Unknown	Beta	Alpha
		MA	MN	BY	Type 2	Unknown	Gamma	Alpha
		MA	MN	KL	Type 3	N/A	Gamma	Beta
		RR	KL	BY	Type 2	121.8	Beta	Alpha
		RR	MN	BY	Type 1	1.9	Gamma	Alpha
		RR	MC	BY	Type 1	99.2	Delta	Alpha
		RR	MN	KL	Type 1	13.9	Gamma	Beta
		RR	MC	KL	Type 1	70.1	Delta	Beta
		RR	MC	MN	Type 2	Unknown	Delta	Gamma
		JN	KL	BY	Type 3	N/A	Beta	Alpha
		JN	MN	BY	Type 2	Unknown	Gamma	Alpha
2001	1	KY	EK	SP	Type 1	Unknown	Beta	Alpha
		KY	FD	SP	Type 2	Unknown	Gamma	Alpha
		KY	FD	EK	Type 2	19.2	Gamma	Beta
		JL	EK	SP	Type 2	Unknown	Beta	Alpha
		JL	FD	SP	Type 1	Unknown	Gamma	Alpha
		JL	FD	EK	Type 2	Unknown	Gamma	Beta
2002	2	SHL	BR	ED	Type 2	Unknown	Beta	Alpha
		SHL	RY	BR	Type 1	Unknown	Gamma	Beta
		SHL	CH	BR	Type 1	Unknown	Delta	Beta

Table 3.1 (continued): List of all rank reversals occurring in groups having male dominance hierarchies during the pre-breeding season of each year

2002	2	SHL	CH	ED	Type 2	Unknown	Delta	Alpha
		SHL	CH	RY	Type 2	Unknown	Delta	Gamma
		JO	BR	ED	Type 1	96.2	Beta	Alpha
		JO	RY	BR	Type 1	24.2	Gamma	Beta
		JO	CH	ED	Type 2	388.1	Delta	Alpha
		JO	CH	BR	Type 2	324.3	Delta	Beta
		QU	CH	ED	Type 1	29.6	Delta	Alpha
		VT	BR	ED	Type 1	159.5	Beta	Alpha
		VT	CH	BR	Type 1	41.8	Delta	Beta
		TO	BR	ED	Type 3	N/A	Beta	Alpha
		TO	RY	ED	Type 1	11.2	Gamma	Alpha
		TO	RY	BR	Type 2	123.6	Gamma	Beta
		TO	CH	ED	Type 2	Unknown	Delta	Alpha
2002	3	CA	MN	KL	Type 1	22.9	Beta	Alpha
		CA	BY	KL	Type 1	83.5	Gamma	Alpha
		CA	BY	MN	Type 1	53.7	Gamma	Beta
2003	2	TO	LE	BR	Type 2	91.1	Delta	Alpha
		TO	RY	ED	Type 1	Unknown	Gamma	Beta
		TO	LE	ED	Type 2	143.4	Delta	Beta
		TO	LE	RY	Type 2	137.3	Delta	Gamma
		KA	RY	ED	Type 2	147.9	Gamma	Beta
		KA	LE	ED	Type 2	42.0	Delta	Beta
		KA	LE	RY	Type 2	48.1	Delta	Gamma
2003	3	JA	KL	CP	Type 1	Unknown	Beta	Alpha
		JA	MN	CP	Type 1	Unknown	Gamma	Alpha
		JA	MN	KL	Type 1	194.7	Gamma	Beta
2004	3	JN	MN	KL	Type 2	Unknown	Beta	Alpha
		HO	MN	KL	Type 2	Unknown	Beta	Alpha

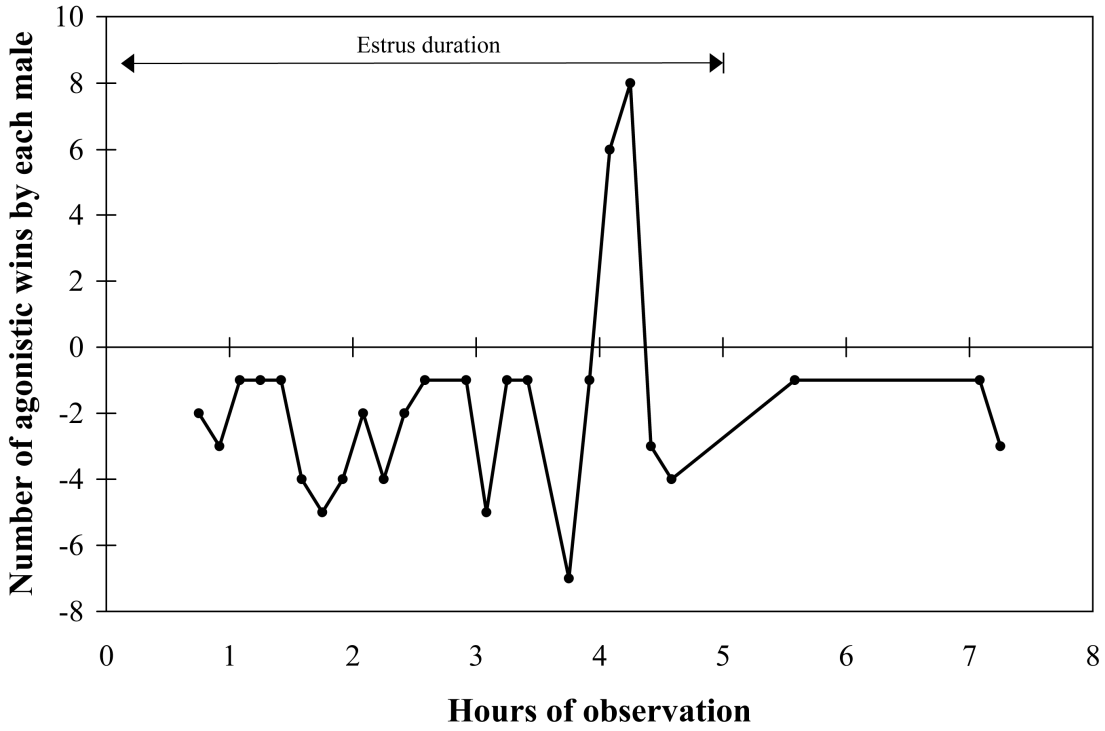

Figure 3.1: "Type 1" rank reversal – example 1. An example of a clearly-delineated rank reversal between two *L. catta* males, RY and BR, in 2002 during the estrus period of female JO in Group 2 (Tables 2.3 and 3.1). The number of wins by each male per 10-minute period are graphed here. All values below zero indicate agonistic wins by the higher-ranked beta male, BR. Values above zero indicate wins by lower-ranked gamma male, RY, and represent a temporary rank reversal between these two males. Time zero marks 0700 hours. Although observations began at 0710, the first agonistic interaction between these two males was not observed until 0744. All estrus activity ceased at approximately 1200, at which time male dominance ranks had already returned to pre-breeding season status.

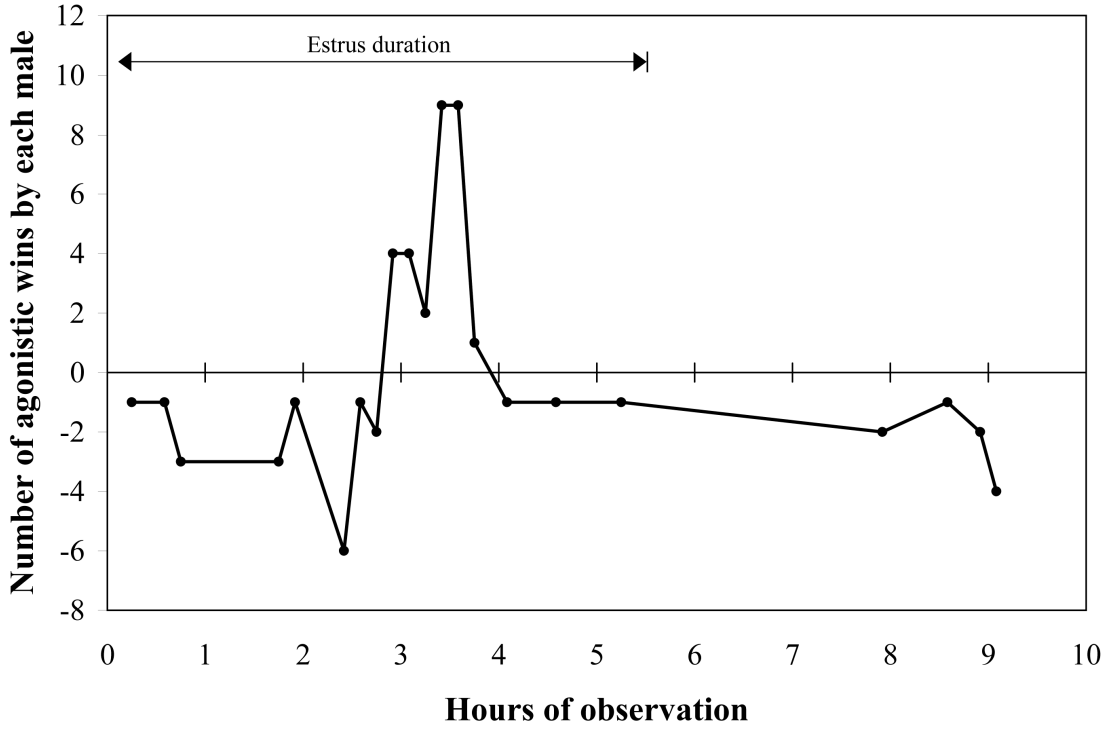

Figure 3.2: "Type 1" rank reversal – example 2. Another example of a clearly-delineated rank reversal between two *L. catta* males, MC and KL, in 2001 during the estrus period of female RR in Group 3 (Tables 2.3 and 3.1). The number of wins by each male per 10-minute period are graphed here. All values below zero indicate agonistic wins by the higher-ranked beta male, KL. Values above zero indicate wins by lower-ranked delta male, MC, and represent a temporary rank reversal between these two males. Time zero marks 0700 hours, when observations began. All estrus activity ceased at approximately 1230, at which time male dominance ranks had already returned to pre-breeding season status as in the previous example.

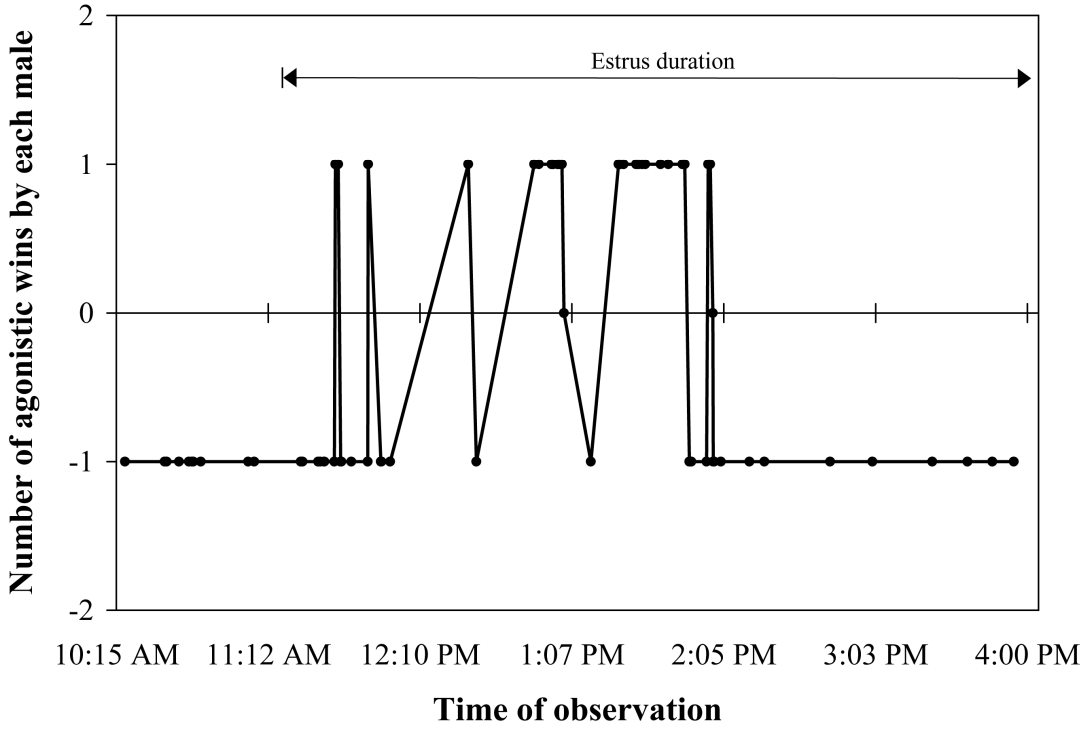

Figure 3.3: "Type 2" rank reversal – example 1. An example of the second form of rank change among male *L. catta* during the mating season: frequent agonistic interactions with variable outcomes. Agonistic wins per male are represented here at the exact time at which they occurred. All values below zero indicate agonistic wins by the higher-ranked beta male, ED. Values above zero indicate wins by lower-ranked delta male, LE. Zero values represent full-contact fights between these males which neither won. This rank reversal took place in 2003, and involved a delta male, LE, and a beta male, ED, during the estrus period of female TO in Group 2 (Tables 2.3 & 3.1). Though data collection began at 0640 that morning, estrus behavior was not observed until 1120. The first recorded agonistic interaction between these males was at 1018. Note that male dominance ranks do not become unstable until after the female enters estrus. When observations ceased at nightfall, the female was still in estrus, though male dominance ranks had already returned to pre-breeding season status.

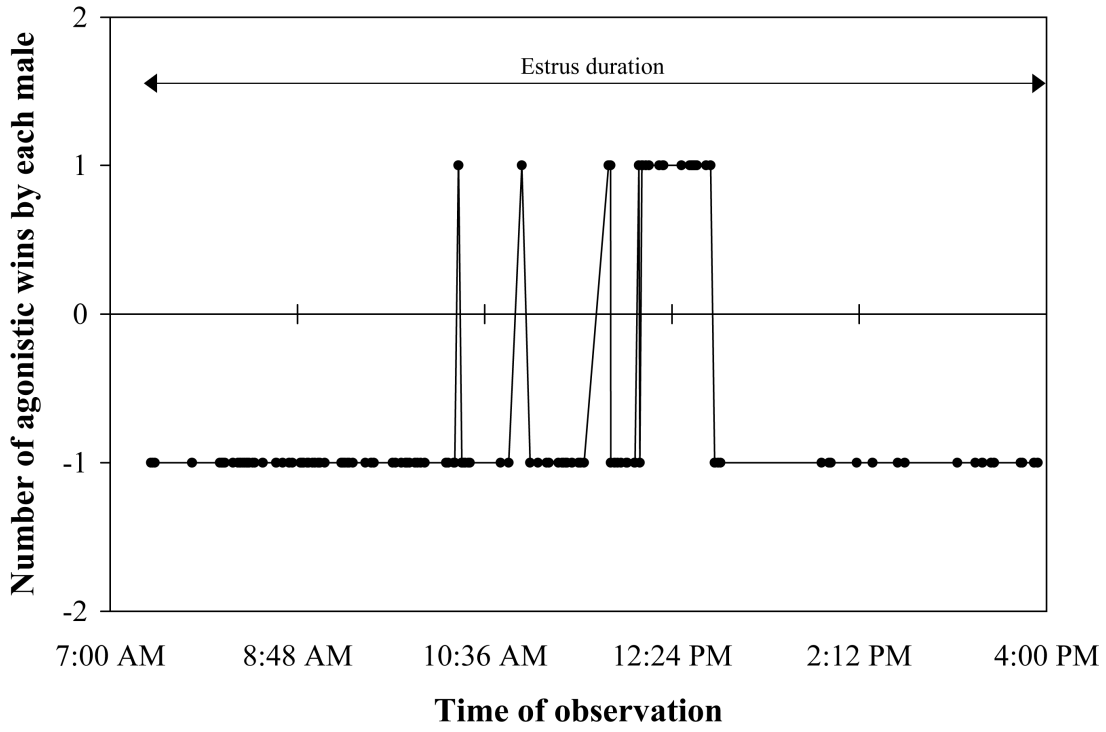

Figure 3.4: "Type 2" rank reversal – example 2. Another example of the second form of rank change among male *L. catta* during the mating season: frequent agonistic interactions with variable outcomes. Agonistic wins per male are represented here at the exact time at which they occurred. All values below zero indicate agonistic wins by the higher-ranked beta male, ED. Values above zero indicate wins by lower-ranked gamma male, RY. This rank reversal took place in 2003, during the estrus period of female KA in Group 2 (Table 2.3). The female was already in estrus when data collection began at 0715 that morning. The first recorded agonistic interaction between these males was at 0723. When observations ceased at nightfall, the female was still in estrus, though the dominance ranks of these two males had already stabilized and returned to pre-breeding season status.

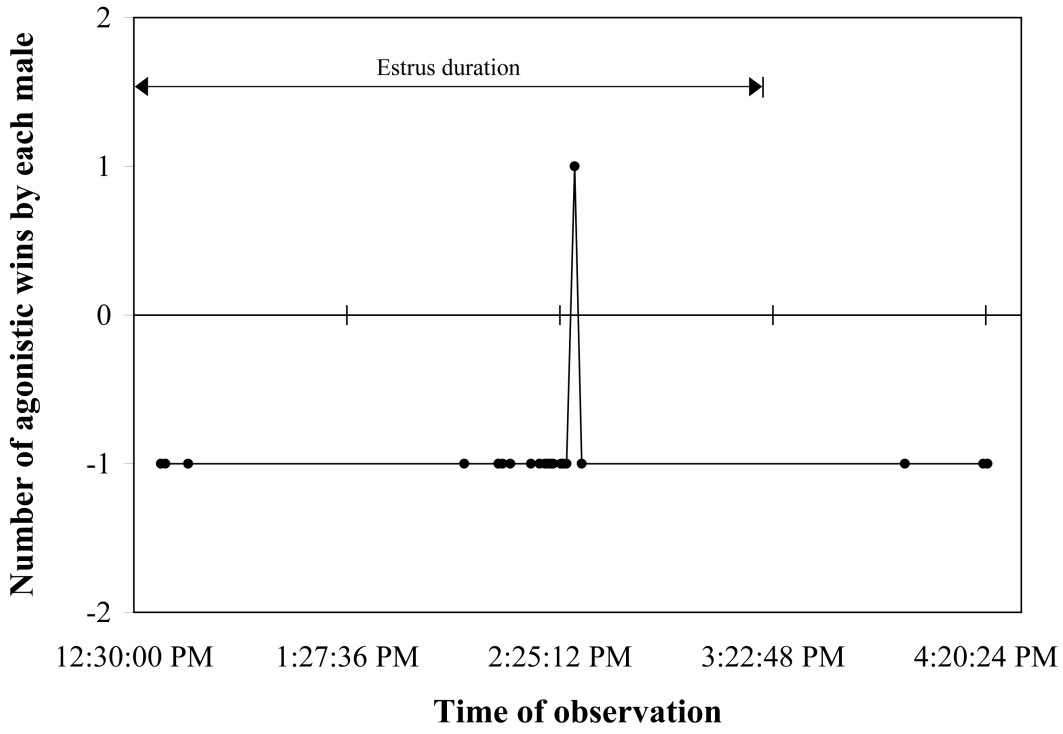

Figure 3.5: "Type 3" rank reversal. This figure portrays the third type of dominance rank change among male *L. catta* during the mating season: a single agonistic win by a lower-ranked male. The instance above occurred in 2001, during the estrus period of female MA in Group 3 (Tables 2.3 & 3.1). Agonistic wins per male are represented here at the exact time at which they occurred. Values below zero indicate agonistic wins by the higher-ranked alpha male, KL. The single value above zero indicates a win by the lower-ranked beta male, MN. The female was already in estrus when data collection began at 1230. The first recorded agonistic interaction between these males was at 1237. When observations ceased, the female was no longer in estrus and the dominance ranks of these two males had returned to pre-breeding season status.

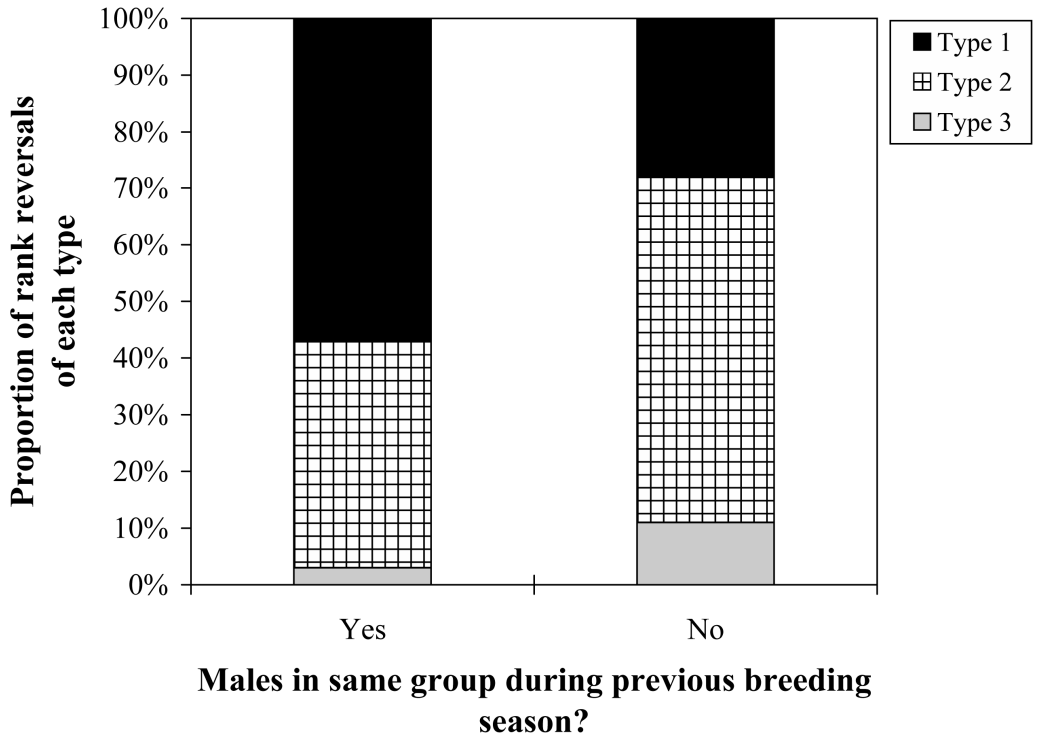

Figure 3.6: Proportion of rank reversals of each type by males who did and did not spend the previous breeding season in the same group. Rank reversal types are as follows: "type 1": clearly-delineated reversals; "type 2": agonistic interactions with highly variable outcomes; "type 3": single win by a lower-ranked male. Data come from Table 3.1. Though the trend is not statistically significant (Friedman's 2-way ANOVA: $\chi^2 = 0.33$, df = 1, $p < 0.564$, NS), males who had not spent a previous breeding season together tended to have more "type 2" rank reversals, indicating greater dominance instability among unfamiliar males.

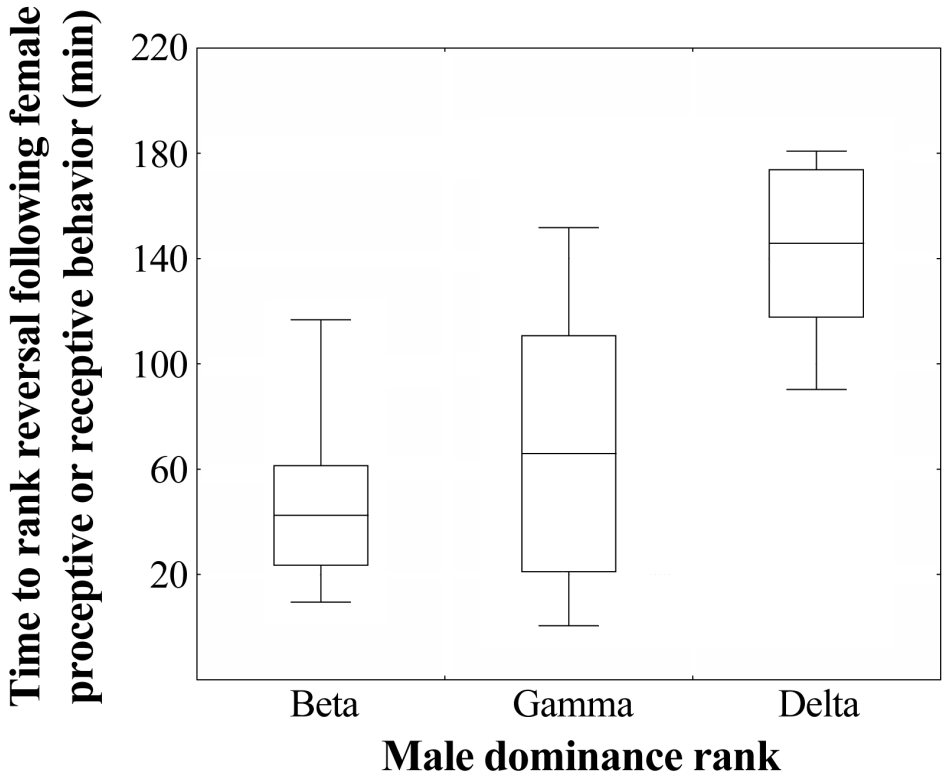

Figure 3.7: Time to rank reversal following receipt of female proceptive or receptive behavior by males of different dominance ranks. For each dominance rank category, a single mean value per male was used. Though higher-ranking males tended to achieve reversals in less time following female proceptivity or receptivity, this trend was not significant (Kruskal-Wallis: $\chi^2 = 4.32$, df = 2, $n_{beta} = 5$, $n_{gamma} = 3$, $n_{delta} = 3$, $p < 0.116$, NS). Whiskers represent maximum and minimum values, lines represent mean values, and boxes represent the standard error of the mean.

CHAPTER 4: MALE INTER-TROOP TRANSFER AND MALE MATING SUCCESS

INTRODUCTION

Sex-Biased Dispersal

Many group-living animals show sex-biased natal dispersal, whereby members of only one sex disperse out of the group into which they are born, often when sexual maturity is reached (Baker, 1978). Several proximate forces can drive dispersal, including competition for resources or increased mating opportunities for dispersing individuals (Dobson, 1982). Dispersal can contribute to gene flow (Lindburg, 1969) and help maintain genetic variation in a population (Howard, 1960). One commonly noted consequence of dispersal is inbreeding avoidance (Packer, 1979a). However, whether dispersal is a specific adaptation to protect against inbreeding depression has been much debated (Moore and Ali, 1984, 1985; Packer, 1985).

Species-specific sex-biased dispersal patterns can be the result of several factors, including the defensibility of food and other resources. Where food is defendable, females may be more likely to remain in their natal groups, as this enables female kin to cooperatively defend such resources (Wrangham, 1980), especially where between-group competition predominates (van Schaik, 1989). Conversely, males may be more likely to remain in natal groups where the development of cooperative male kin bonds provide selective advantages to males, such as when affiliation among male kin enables groups of related males to defend reproductive females (e.g. Strier, 1994a). Among mammals in

general, male-biased natal dispersal is more common than female-biased dispersal (Greenwood, 1980, 1983). The same trend is found among primates (Greenwood, 1980; Pusey and Packer, 1987), though female-biased dispersal and dispersal by both sexes occur in some species (Harcourt, 1978; Harcourt et al., 1976; Glander, 1980, 1992; Moore, 1984; Clutton-Brock, 1989b; Goldizen and Terborgh, 1989; Watts, 1990; Garber, 1994; Strier, 1994b, 1999; Sterck, 1997; Pope, 2000, Isbell, 2004).

One particular taxonomic group, the Malagasy prosimians, shows much variability in sex-biased dispersal patterns, but many show some degree of male dispersal (e.g., the red-fronted (rufous) lemur, *Eulemur fulvus rufus*: Merenlender, 1993; Overdorff et al., 1999; mongoose lemur, *E. mongoz*: Curtis and Zaramody, 1998; red-bellied lemur, *E. rubriventer*: Merenlender, 1993; Overdorff, 1992; Alaotran gentle lemur, *Hapalemur griseus alaotrensis*: Nievergelt et al., 2002; eastern lesser bamboo lemur, *H. g. griseus*: Grassi, 2001; ring-tailed lemur, *Lemur catta*: Budnitz and Dainis, 1975; Jones, 1983; Sauther, 1991; Sussman, 1991, 1992; Gould, 1994, 1997; grey mouse lemur, *Microcebus murinus*: Radespiel et al., 2003; Milne-Edward's sifaka, *Propithecus diadema adwardsi*: Wright, 1995; Verreaux's sifaka, *P. verreauxi*: Richard, 1978; Jolly et al., 1982a; Richard et al., 1993; Kubzdela, 1997; captive black and white ruffed lemurs, *Varecia variegata variegata*: White et al., 1993).

Documenting Dispersal Patterns: Difficulties and Alternatives

Documenting natal dispersal and subsequent inter-troop transfer of individuals over time is difficult in the wild under most circumstances. Dispersing animals must be

identifiable, requiring that they have individually unique characteristics or be marked via a capture process and/or fitted with a transmitter (Honess and MacDonald, 2003), which can be logistically difficult to achieve and potentially socially disruptive for the animals involved. Migrating individuals must also be located following their departure from a group, which may prove nearly impossible under field conditions where animals travel extremely long distances or can migrate out of a study area or reserve (e.g., the ringtailed lemur, *Lemur catta*: Gould et al., 2003). Consequently, male migration in the wild is often documented primarily by the arrival of new immigrants into a social group or by opportunistic sightings of males in their new groups. When males disappear it is frequently unknown whether the disappearance is due to death or emigration (e.g, red-fronted lemur, *Eulemur fulvus rufus*: Overdorff et al., 1999).

In such situations, studying male inter-troop movement in a non-endemic area might prove to be useful, as such data can augment what is known about the behavior of a species in its natural habitat. Several locations currently exist which support free-ranging primates in non-endemic areas. One of the best known non-endemic primate colonies is the Cayo Santiago rhesus macaque (*Macaca mulatta*) colony that was established by C.R. Carpenter in 1938 (Rawlins and Kessler, 1986). At this site, macaques are free to transfer between groups as they do in the wild (Lindburg, 1969), and studies of male dispersal at this site have yielded useful comparative data for this species (Colvin, 1983, 1986; Berard, 1989; Waitt et al., 2004). Another such location is St. Catherines Island, Georgia (USA), a site which supports a colony of free-ranging ringtailed lemurs, *Lemur catta* (Keith-Lucas et al., 1999).

This Study: Male Dispersal Patterns on St. Catherines Island

The present study analyzed patterns of male dispersal in the *L. catta* colony on St. Catherines Island, and compared patterns of male inter-troop movement at this location to what is known about *L. catta* male dispersal patterns in the wild. Though St. Catherines is a non-endemic environment, data from this site can add to what is currently known about the dispersal behavior of *L. catta* males, as it provides a kind of natural experiment in which the parameters of male inter-troop movement can be studied under known environmental conditions, which include food abundance due to provisioning and a limited population size due to the isolation of the lemur groups on an island.

Of particular interest to this dissertation was the effect of male dispersal on male mating success. Sauther and Sussman (1993) identify male inter-troop movement as a mating strategy of *L. catta* males. Accordingly, it might be expected that *L. catta* males show increased mating success after transferring into a new social group. Indeed, studies of other primate species suggest that males can markedly increase their mating success by transferring into new groups (e.g. baboons, *Papio cynocephalus*: Alberts and Altmann, 1995). No study has heretofore measured male mating success before and after inter-group transfers in *L. catta* using a large sample size of male migration events.

Background: The Ringtailed Lemur (*Lemur catta*)

Lemur catta are Malagasy prosimian primates that live in multi-male, multi-female groups which range in size from 5 to 27 individuals, with group sex ratios approximating 1:1 (Jolly, 1966; Sussman, 1974, 1991; Budnitz and Dainis, 1975; Mertl-

Milhollen et al., 1979; Jolly et al., 1982b; Sauther et al., 1999; Gould et al., 2003; Pride, 2003, 2005). Within each sex a dominance hierarchy exists, and reproductively mature females dominate troop males (Jolly, 1966; Taylor and Sussman, 1985; Taylor, 1986; Kappeler, 1990a; Pereira et al., 1990; Sauther, 1992; Gould, 1994; Sauther et al., 1999). A troop is typically comprised of related females and their offspring and immigrant non-natal adult males (Jolly, 1966; Sussman, 1992).

This species breeds seasonally, with females only copulating during estrus, which lasts less than one day in most cases (Jolly, 1966, 1967; Evans and Goy, 1968; Van Horn and Resko, 1977; Koyama, 1988; Sauther, 1991; Koyama et al., 2001; Pereira and Weiss, 1991). *L. catta* experience asynchrony in estrus (Pereira, 1991), and captive studies indicate that female *L. catta* are polyestrus, cycling up to three times per season if kept under natural light conditions, with each cycle being separated by an average of 39 days (Evans and Goy, 1968). Most females conceive during their first estrus cycle of the season in the wild (Sauther, 1991) and on St. Catherines Island (Parga and Lessnau, 2005). Female *L. catta* often mate with more than one male during estrus, and mate choice has been documented in captive (Van Horn and Resko, 1977; Taylor and Sussman, 1985; Taylor, 1986; Pereira and Weiss, 1991) and wild individuals (Koyama, 1988; Sauther, 1991; Gould, 1994).

Male *L. catta* in the wild typically migrate between groups in the birth and lactation season, but migration and temporary male extra-troop visits can also take place throughout the months preceding and during the mating season (Budnitz and Dainis, 1975; Jones, 1983; Gould, 1994, 1997; Sauther, 1991; Susssman, 1991, 1992). Males in

the Beza Mahafaly Special Reserve in Madagascar first transfer from their natal group between three and five years of age (Sussman, 1992), migrate approximately every three and a half years, and usually attempt to transfer into new groups in pairs or small groups (Budnitz and Dainis, 1975; Jones, 1983; Sussman, 1991, 1992; Gould, 1994, 1997).

Is Male Inter-Troop Movement a Successful Mating Strategy in *L. catta*?

This is the first study to compare patterns of male inter-troop movement in a non-endemic *L. catta* colony with published data from wild individuals of this species in Madagascar. Males in the wild cannot often be followed over multiple years due to their tendency to migrate out of reserves or areas of study (Sussman, 1991, 1992; Gould, 1994; Gould et al., 2003). In contrast, St. Catherines Island provided an apt location for a study of male dispersal behavior, because the eventual destination of all migrating males is known due to the ability to radio track collared individuals at this site. Also, because the colony is maintained on an island, males cannot migrate out of the study area. Due to its focus on mating behavior and its long-term duration, this study was able to compare the effects of male inter-troop movement on male mating success for several different males across a multi-year period.

The first goal of this chapter was to compare patterns of male inter-troop transfer in the St. Catherines Island colony to patterns of male transfer among wild *L. catta* with respect to: 1) age at first dispersal (natal dispersal), 2) mean number of years of troop tenure between non-natal transfers, 3) time of dispersal (seasonality of male transfer), and

4) whether males typically transfer alone or in groups. The second goal was to evaluate the success of inter-group transfer as a male mating strategy in this primate colony.

METHODS

Definition of Dispersal

Following Bekoff (1977), *dispersal behavior* by an individual is defined as, "...movements away from its own (or group) home range into another area" (p.715). Whereas the definition given by Bekoff (1977) specifically applies to adult individuals, in this chapter the term is applied regardless of the age of the dispersing individual and describes the movement of individuals who leave both natal and non-natal groups of residence. A distinction is made between *natal dispersal*, which is the emigration of males out of the group in which they were born, and *non-natal dispersal* (sometimes termed secondary dispersal), which is the emigration of males from a non-natal group (Pusey and Packer, 1987). In this chapter, the terms *inter-troop movement* and *migration* are also used interchangeably with dispersal to denote the movement of males between social groups, and can apply to both natal dispersal and non-natal dispersal by males.

Study Site and Study Animals

St. Catherines Island (located at 31º 40' N latitude, 80º 41' W longitude) is a privately-owned, largely undeveloped semi-tropical barrier island measuring 2,900 hectares, with a mixture of habitats, including pine, oak and palmetto forests, and open pastures as well as savanna and marsh (Thomas et al., 1978; Thomas, 1988). A colony of

L. catta was started by the Wildlife Conservation Society (WCS) at this location in 1985 with the release of a founder group of six lemurs (Keith-Lucas, et al., 1999). Although most individuals in the island colony are descendants of females in the original founder population, there have been two instances in the colony's history when an unrelated female and her offspring were added to the population (Parga and Lessnau, 2005). With the addition of several unrelated males throughout the years to increase genetic diversity in this population, the lemur colony grew to over 75 individuals in four free-ranging groups (Parga and Lessnau, 2005). Of all males that have resided in the free-ranging colony (n = 87), 17 were non-natal (added by WCS personnel), and 70 were born into the colony. One of these troops was relocated in October 2002 to a captive zoological institution (Table 2.1), and three free-ranging troops now remain in the island population.

L. catta on St. Catherines Island forage on naturally-occurring vegetation, show ranging behaviors, and groups have established home range areas (Dierenfeld and McCann, 1999; Keith-Lucas et al., 1999). Throughout the course of the present study, the lemurs were provisioned once daily with food (a mixture of monkey chow and fruits and/or vegetables) and water at heated shelter sites that they were able to enter and exit freely. All adult lemurs were fitted with uniquely-colored Telonics radio collars (Mesa, AZ) by WCS personnel. Subadults and small adults were often fitted with nylon collars. Differences in physical characteristics and shaving patterns were used to identify uncollared animals.

Each of the four free-ranging groups on St. Catherines was studied as part of this project, though different groups were studied in each year. Table 2.1 shows the groups

that were studied during the start and middle of the breeding season in each year of this project (spanning late October-December). Table 2.2 shows the composition of each study group in early October (prior to the start of the mating season) of each year. Each lemur group had between 5-11 females one year of age or older, and 2-4 non-natal males one year of age or older (Table 2.2).

Records on Troop Composition and Male Inter-Troop Movement

WCS personnel have kept records of all lemur births and deaths since the start of the St. Catherines Island colony. These records allow for determination of matrilineal relatedness among individuals. At present, offspring paternity is unknown. In 1997, R. Lessnau, senior zoologist on St. Catherines, began keeping daily records on the composition of all lemur groups, which included recording data on male inter-troop movement. WCS staff visited each lemur group site daily, and verified the health status and location of all individuals, noting such occurrences as the presence of a visiting male from a neighboring troop, or conversely, the absence of individuals on particular days. If a group was not in the vicinity of its feeding station upon this visit (or if an individual was missing from the troop), an effort was made by WCS staff to locate the troop or individual via radio telemetry. In this way, instances of male inter-troop movement and troop fission on St. Catherines Island (Hungerford et al., 2001) have been documented. Data on male inter-troop transfers collected between 1997-2005 were used in this analysis.

Colony Management on St. Catherines Island

Because relatedness among lemurs in the colony is estimated to be fairly high, the WCS has occasionally removed individuals to reduce potential inbreeding in the population. Males who failed to join a social group upon dispersing (i.e. if a male migrated to a part of the island where no lemur troops range) were removed. Additionally, for management purposes, some subadult males have been removed from their natal groups prior to migration (Lessnau, pers. comm.).

Male Troop 'Visits' Versus Inter-Troop Transfers

Male extra-troop 'visits' were considered separately from inter-group transfers. Male visits were those that lasted from less than one day to one week in length, and males returned to the group from which they came. Because data on male visits were not consistently collected by all WCS staff members, these temporary visits were not considered in the analyses. In contrast, inter-troop transfers were routinely recorded by WCS personnel on the island. Inter-troop transfers are defined as migration events in which males stayed in their new groups for at least one month or more before transferring again. No male stayed in a new group for more than one week but less than one month (Lessnau, unpub. data).

Data Collection on Mating and Social Behavior

A. Breeding Season

Due to photoperiodic regulation, reproduction in *L. catta* on St. Catherines is approximately six months out-of-phase with the timing of these events in Madagascar, the endemic habitat of this species (Rasmussen, 1985). Mating behavior is limited to the fall and winter months (September-February) in the northern hemisphere if exposed to natural light (Evans and Goy, 1968; Van Horn, 1975). Data on mating behavior were collected during five consecutive breeding seasons: October-December 2000-2004, with additional data collected on mating behavior late in the breeding season of one year, during January-February 2004.

During breeding periods, data were collected daily from "dawn to dusk" using 'all-occurrences' sampling (Altmann, 1974) of agonism and reproductive behavior. In mating contexts, the following behaviors were recorded (in addition to recording the agonistic behaviors listed in section "B. Non-Breeding Season" below): jump-fights, mounts, thrusting, and female sexual presents. If observable, penile intromission, ejaculation, and copulatory plug displacement (Parga, 2003) were also recorded, though observation conditions did not always allow these more detailed sexual behaviors to be verified. Ejaculation was indicated by the presence of semen in the female's peri-vaginal area, and/or on the tip of the male's penis. The start time (and stop time, if appropriate) of each behavior was recorded in seconds. Behavioral estrus was indicated by proceptive (sexual solicitation) or receptive (allowance of male mounting) behavior (Beach, 1976).

During the 2001 through 2004 breeding seasons, one to two field assistants helped monitor groups for estrus behavior and collect social and reproductive data. One observer was stationed per group unless a female was in estrus in one of the groups, in which case two observers paired up at the group with the estrus female.

B. Non-Breeding Season

During the pre-breeding months of each year (June-September in 2000 and 2004, and September-October 2001–2003), data on social behavior were collected approximately five days per week between the hours of 0600 and 1900, with the majority of samples collected between 0800 and 1600. Information on dominance relationships among males was gathered during this time via two main sampling techniques: continuous-time focal animal sampling, and 'all-occurrences' sampling for agonism (Altmann, 1974). Each sampling technique was performed separately, alternating between the two sampling types throughout the day. Each type of sample lasted for 20 minutes during 2000-2001, and was thereafter shortened to 15 minutes in duration. Focal sampling order was randomized, with no more than two samples per individual per day.

During focal samples, the following 'state' behaviors (Martin and Bateson, 1986) were recorded to the nearest second: rest, travel, feed, auto-groom, and allo-groom. The following 'event' behaviors (Martin and Bateson, 1986) were scored: approach, defecate, urinate, scent-mark (ano-genital, palmar, shoulder, tail), approach-withdraw, bite, chase, cuff, fight, grapple, lunge, nose-push, push, stink-fight, and take food (Jolly, 1966; Petter and Charles-Dominique, 1979; Taylor, 1986; Gould, 1994; Pereira and Kappeler, 1997;

Parga, 2002a). *Ad libitum* data were collected at all times during all seasons of the year in both non-mating and mating periods to record sporadic or infrequent events such as predation attempts on the lemurs, instances of mobbing, and alarm or howling vocalizations.

Definition of Mating and Male Mating Success

Mating is defined here as a male mounting a female. A more detailed definition such as 'mounting with penile intromission' or 'mounting with ejaculation' was not used because observation conditions did not always permit documentation of penile intromission or ejaculation during mounts. Male mating success is defined as the number of females (or conversely, the proportion of group females observed to enter estrus) a male was observed mounting in a single mating season. Though male reproductive success (number of offspring sired) would be a more desirable measure to use in analyses, paternity data are not available at the present, limiting this analysis to male mating success.

Data Analysis

To calculate the mean age at first transfer (natal dispersal), only males born during 2003 and earlier were included. To calculate mean number of years of group tenure between non-natal transfers, all transfers in which the immigration date and emigration dates were known were used, excluding the troop tenure in the final group of residence for males who were removed due to population management, and males who

died (as their troop tenure may have been significantly longer than it was at the time of death).

All "decided" agonistic interactions (Hausfater, 1975; Pereira and Kappeler, 1997) between males were used to determine male dominance ranks for each group. Agonistic outcomes for each male dyad were tallied in a matrix, as described in Bramblett (1994). This method allows for a net dominance score to be calculated for each individual and a corresponding rank to be assigned to each based upon their relative dominance score.

Where inferential statistics were used, non-parametric tests were employed (i.e., Binomial test, Chi-square goodness of fit, Friedman's 2-way ANOVA, Kolmogorov-Smirnov, Mann-Whitney *U*, Wilcoxon signed-rank sum). All tests were two-tailed, and the level of significance was set at 0.05. All means are reported with the standard error of the mean (SEM). Statistical tests were performed using Statistica, version 5.5.

RESULTS

Natal Male Dispersal

A total of 30 transfer events were recorded in this study. Approximately half of the transfers (n = 17) were instances of dispersal out of the natal group (Table 4.1). Males migrated out of their natal groups between the ages of 1.6 years and 3.0 years (Figure 4.1), and the mean age of transfer out of the natal group was 2.2±0.1 years. The majority of males (88.2%) migrated out of the natal group before reaching three years of

age. All remaining males migrated out of their natal group shortly after reaching their third year.

There was only a single male in the history of the colony who remained in his natal group beyond age three (male JY from Group 1, Table 2.2). It is unknown how long this male would have remained in his natal colony before migrating, because he was removed from the colony in 2002 when his group was relocated to a captive zoological institution. At the time of the group's removal from the island colony, the male was three years, seven months old, and he had not yet migrated out of his natal group.

Avoidance of Natal Groups as Transfer Destinations

A striking trend was that no male ever migrated back to his natal group (Tables 4.1 & 4.2), even though some males migrated several times during the course of the study period (e.g., KL transferred four times, see Table 4.2). In search of a group in which to immigrate, six males even migrated beyond the current home ranges of the free-ranging groups to areas of the island with no lemurs, which necessitated their removal from the island population by colony management (Table 4.1 & 4.2).

Frequency of Transfer and Duration of Troop Tenure Between Transfers

Adult males (aged 2 years and older, n = 9) transferred between non-natal groups approximately every 3.2 years. Mean male group tenure was 2.2 ±0.6 years (n = 11), but this value includes data on males who remained in some groups for just a few months before migrating again (Table 4.2). A reanalysis excluding cases in which males

transferred more than once during the same season showed that mean troop tenure for males who spent at least one mating season in a troop before migrating was 3.4±0.6 years (n = 7, Table 4.2).

Troop tenure for males who migrated into a troop as part of a natal migration was known conclusively for six males, and was highly variable. The maximum male tenure in a troop following a transfer from a natal troop was 5.8 years, and the minimum was 2 months (Table 4.2). The mean troop tenure spent in a group following migration from the natal troop was 1.8±0.9 (Table 4.2).

Seasonality of Male Inter-Troop Transfer

There was a definite seasonal peak in male dispersal at this site. The majority (80%) of male migrations occurred between the months of March and June (Figure 4.2), which coincides with the peak birth period on St. Catherines (Parga and Lessnau, 2005). Both male natal and non-natal dispersal showed this seasonal peak. A few male migrations occurred during the breeding season at this location, in the months of November and January (Figure 4.2).

The two male migrations that occurred during the month of November deserve special mention, as they were facilitated by management intervention in group dynamics. During 2004, two resident adult males of Group 3 became seriously injured during an aggressive interaction over access to the first female to enter estrus in this social group. Following veterinary attention, these two males (the only non-natal males in the group) were placed within the shelter site that serves as the location of daily food provisioning,

and were not allowed to free-range with the group for several days following this incident. Within two days of the injured resident males being locked in the enclosure, two young males from Group 2 (CP and MX, aged two and one years, respectively, Table 2.2) migrated into Group 3, and remained in this group for the remainder of the breeding season until they were permanently removed by management the following spring.

Do Males Transfer Alone or Together?

Whether or not males transferred together or alone was known for 16 of the 17 natal male transfers documented (Tables 4.1 & 4.2). For natal male transfers, males were significantly more likely to transfer with one or two other males than alone (Binomial test, $n = 16$, $x = 2$, $p = 0.0018$). In contrast, non-natal transfers were no more likely to involve groups of males than lone males (Binomial test, $n = 13$, $x = 5$, $p = 0.157$, NS).

Natal males transferred with a birth cohort member in 38% of cases, and with an older or younger matrilineally-related natal male in 69% of natal transfers (Table 4.1). In all other instances in which a natal male transferred with one or two non-natal males, the possibility exists that the natal males (MN, FZ, and WD) transferred with their fathers. Each of the non-natal males who accompanied the younger males' natal dispersal (KL, BR & ED, and BY, respectively; Table 4.2) were in the male's natal group at the time that the younger male was conceived, and were old enough to sire the natal male in question (refer to Tables 2.1 & 2.2 for male age and group membership information).

Males leaving their natal groups were especially likely to transfer with one male than to transfer alone or with two other males (Chi-square goodness of fit: $\chi^2 = 16.63$, df

= 2, $p < 0.0003$; Figure 4.3). However, in non-natal transfers, males were no more likely to disperse with one or two other males than alone (Chi-square goodness of fit: $\chi^2 = 2.00$, df = 2, $p < 0.368$, NS). Male age did not affect whether males more likely to transfer with other males than alone (Kolmogorov-Smirnov: $n_1 = 7$, $n_2 = 22$, $p > 0.10$, NS; Figure 4.4).

Male Dominance Status and Transfer Behavior

An analysis of male dominance rank by male inter-troop transfer behavior shows that higher-ranking males were significantly more likely than lower-ranking males to migrate out of a social group (Friedman's 2-way ANOVA: $\chi^2 = 4.00$, df = 1, $p < 0.046$; Figure 4.5). Unfortunately, direct comparisons of male dominance rank prior to and following a migration event could not be performed, as such data were not available for more than a single male (KL) who was known to hold alpha status in his pre-migration group (Parga, unpub. data) to holding beta status in his new group (Table 2.3) when he transferred between Groups 2 and 3 during April 2001 (Table 4.2).

Male Mating Success and Inter-Troop Transfer

Among all natal males observed during the mating season in this study, no male showed any degree of mating success in his natal group. However, every natal male who transferred into a new social group showed some degree of mating success in his new troop (Table 4.1). Some males showed a minor degree of mating success, for they mated with only one female in the social group (EK and FZ, Table 4.1), whereas others showed

a remarkable number of female sexual partners, mating with the majority of group females observed to enter estrus (CP, Table 4.1).

In the first breeding season following their natal migration into a troop, males used a variety of mating strategies, including holding alpha status, achieving rank reversals, and performing sneak copulations (Figure 4.6; Table 2.3). Four males leaving their natal troops transferred into groups without a stable male dominance hierarchy, and gained copulations during the mating season via aggressive male-male competition. Because the aggressive male mating strategies previously described in Chapter 2 (i.e., alpha, rank reversal) apply specifically to cases where male dominance hierarchies existed, the four males who migrated into groups without male dominance hierarchies were described as using a generalized aggressive mating strategy (Figure 4.6). The number of copulations gained through the use of aggressive strategies versus non-aggressive strategies (i.e., sneak copulation) following a natal male transfer were compared. Males were no more likely to use aggressive versus non-aggressive strategies as recent immigrants from a natal group (Chi-square goodness of fit test: $\chi^2 = 2.57$, df = 1, $p < 0.109$, NS).

For non-natal transfers, mating success data were available for only two males in the breeding season before and following a transfer (Table 4.2). In both cases, males had poorer mating success in the breeding season preceding their transfer, and had higher mating success in the new groups that they joined – both mated with a greater number of (and a larger proportion of) females in their new social group as compared with their old group (Tables 4.2 & 4.3). The mean number of females with whom males were observed

mating in the breeding season prior to a transfer was 1.8±0.6 (n = 5) as opposed to 3.0±0.4 (n = 4) for males who recently joined a new social group. The overall percentage of females mated was likewise notably lower in seasons prior to a transfer (58.3±13.3%) as opposed to following a transfer (81.3±12%).

However, a more comprehensive analysis of male mating success and migration behavior should consider not only those males who migrated, but those who did not migrate from one year to the next. Therefore, male mating success in breeding seasons followed by migration were compared with male mating success in breeding seasons after which males remained in their groups (Table 4.3). No significant difference was found in the mating success of males who stayed following a mating season and the mating success of males who left following a mating season. This finding holds true for both measures of mating success: overall number of females mated (Mann-Whitney: $n_1 = 5$, $n_2 = 26$, $U = 44.5$, $p = 0.28$, NS) and the proportion of group estrus females mated (Mann-Whitney: $n_1 = 5$, $n_2 = 26$, $U = 61$, $p = 0.86$, NS).

Group Sex Ratios and Male Transfer Behavior

Males who remained in their social groups were no more likely to come from groups with more favorable sex ratios (fewer males per female) than were males who migrated (Kolmogorov-Smirnov: $n_1 = 5$, $n_2 = 26$, $p > 0.10$, NS; Table 4.3; Figure 4.7). Males did not transfer between groups having significantly different numbers of females, whether group females aged two years and older were considered (Wilcoxon: $Z = 0.306$, $n = 10$, $p < 0.76$, NS), or females one year and older (Wilcoxon: $Z = 1.89$, $n = 10$, $p <$

0.06, NS). Analyses were run twice with the one-year female age class alternately excluded and included because females can mate at one year of age on St. Catherines, but most do not conceive at this young age (Parga and Lessnau, 2005). A comparison of sex ratios within each male's pre-migration group and post-migration group also showed no significant differences, whether one-year old females were included (Wilcoxon: $Z = 1.12$, $n = 10$, $p < 0.26$, NS), or excluded so that only females two years of age and older were considered (Wilcoxon: $Z = 1.83$, $n = 10$, $p < 0.067$, NS). However, males were significantly more likely to transfer to a group with fewer non-natal males than the group which they left (Wilcoxon: $Z = 2.04$, $n = 10$, $p < 0.042$; Figure 4.8). Therefore, the number of non-natal males per group appeared to be the key variable determining male transfer decisions for non-natal male migrations.

DISCUSSION

Age at Natal Transfer

In the wild, male *Lemur catta* often leave their natal groups for the first time between the ages of three and five years, and most leave in their third or fourth year (Sussman, 1992). In contrast, on St. Catherines Island, males leave their natal groups between the ages of two and three, with most leaving at the age of two years. Natal dispersal is therefore an event that occurs earlier in the lives of males in this provisioned colony than in the wild.

If attainment of sexual maturity is one of the physiological correlates of male natal dispersal, males in this colony might be expected to migrate sooner than males in

the wild because males on St. Catherines likely reach sexual maturity at an earlier age due to enhanced nutrition via provisioning. Male *L. catta* reach puberty (as evidenced by the presence of descended testicles and the onset of genital scent-marking) at 15 months of age in provisioned groups (Pereira, 1993a), and at 20 months in the wild (Sauther, unpub. data). Although it is unknown whether males at these young ages can impregnate females, a yearling male in this study was observed to mate to ejaculation (male MX, Table 2.3). This male performed all the species-typical sexual behaviors of an older adult male, including tail-waving at the female (Jolly, 1966), performing multiple mounts as part of the same copulatory sequence (Sauther, 1991), and displacing a previous male's sperm plug prior to ejaculating (Parga, 2003). Where this male's behavior differed from fully adult males was in his avoidance of male-male competition, for he continually used the strategy of sneak copulation (Chapter 2, Table 2.3).

Early attainment of sexual maturity due to nutritional abundance is seen among females on St. Catherines Island, where the primiparous age (age at first birth) is reached at two years (Parga and Lessnau, 2005) as compared three years of age for unprovisioned females in the wild (Sussman, 1991; Koyama et al., 2001). This same advanced trajectory for the early attainment of sexual maturity likely exists for males as well. Therefore, behaviors associated with the attainment of male sexual maturity such as natal dispersal might be expected to be similarly affected by increased food availability (and the subsequent nutritional gains) brought about by provisioning.

Another likelihood is that the earlier natal migration on St. Catherines is due to sex ratio differences between this provisioned colony and the wild. In wild *L. catta*

groups there is an approximate sex ratio of 1:1 (Jolly, 1966; Sussman, 1974, 1991; Mertl-Milhollen et al., 1979; Gould et al., 2003). However, on St. Catherines, group sex ratios are strongly female-biased (Table 2.2). Accordingly, because there are fewer resident males within groups to repel prospective immigrants, natal males may be more easily able to enter into new social groups, and may be more likely to attempt transfers at an earlier age than in Madagascar.

Mean Time to Inter-Troop Transfer

On St. Catherines, the time males spent in their new groups after leaving their natal groups was highly variable. The longest a male spent in his new social group after leaving his natal group was nearly six years, though other males stayed for one to three years. Some males stayed in their new group for just a few months, then transferred again in the same season, presumably in search of a more desirable group of residence. This pattern of males staying in proximity to a new social group for a short time has also been seen in Madagascar (Jones, 1983; Sauther, 1991; Sussman, 1991, 1992; Gould, 1994).

Considering all male migrations (and both natal and non-natal transfers), males on St. Catherines Island transfer between groups about as frequently as they do in Madagascar. In Beza Mahafaly, adult males reportedly migrate between groups about once every 3.5 years (Sussman, 1992) as compared to once every 3.2 years on St. Catherines. Adult males also only remain in a social group for about 2.8 years in Beza (Sussman, 1992), which is similar to the mean length of troop tenure for adult males on

St. Catherines, which is 2.2 years. However, just as on St. Catherines, there is much inter-individual variation among *L. catta* males with respect to these parameters. For example, though males typically tend to transfer between groups in the wild every few years, some males remain in social groups for many years (Gould, 1994).

For males who do migrate out of a social group after only a few years, such a strategy might be beneficial in incest avoidance. For a male *L. catta* who has sired offspring within a troop, remaining in that troop for only a few years before migrating would result in the male's departure coinciding with the approximate time his daughters would reach sexual maturity (Sussman, 1992). On St. Catherines, females can mate for the first time at the age of one, and have their first infant at age two (Parga and Lessnau, 2005). Therefore, male inter-troop transfer after just a few years' tenure in the group may function to decrease the possibility of incest, though there would be some overlap in male troop tenure and the sexual maturity of potential daughters.

In general, male dispersal every few years may help males produce a more genetically diverse set of offspring across a their lifetime. Although the lifespan of male *L. catta* is incompletely known in the wild, the oldest living female of known age in the Beza Mahafaly population was eighteen years old, and males are thought to have even shorter lifespans than females (Gould et al., 2003). In the St. Catherines Island population, only a few males survive into their teens, with most males surviving for a much shorter period of time than this (Lessnau, unpub. data). Therefore, transferring every few years between groups might be an adaptive male strategy from the perspective of offspring genetic diversity.

Seasonality of Male Inter-Troop Transfer

In some primates having male dispersal, male inter-troop movement occurs primarily during the breeding season (e.g. Hanuman langurs, *Presbytis entellus*: Borries, 2000; rhesus macaque, *Macaca mulatta*: Boelkins and Wilson, 1972). In contrast, among *L. catta* on St. Catherines Island the majority of male inter-troop movement coincided with the months surrounding the peak birth period (March through June: Parga and Lessnau, 2005), while a few instances of male inter-troop movement occurred during the mating season. This seasonal pattern of male inter-troop movement is similar to the seasonality of male dispersal observed in Madagascar, though the timing of reproductive events (and coincident behaviors, such as male migration) are shifted approximately six months because reproduction is controlled by photoperiod (Van Horn, 1975; Van Horn and Eaton, 1979; Evans and Goy, 1968; Rasmussen, 1985). Male inter-troop movement events (including temporary male visits) can occur among wild *L. catta* males in the months surrounding the birth and lactation season, and the months prior to and during the mating season (Budnitz and Dainis, 1975; Jones, 1983; Sauther, 1991; Sussman, 1991, 1992; Gould, 1994, 1997). Therefore, the overall seasonality of male migration on St. Catherines is similar to that observed in Madagascar, though events occur in different months across the two localities due to a hemisphere shift.

One potential adaptive explanation for why male inter-troop transfers occur during the birth season in this species is that this pattern of male migration provides opportunities for males to commit infanticide (van Schaik, 1996). Proponents of sexually-selected male infanticide in *L. catta* suggest that one strategy for males is to

migrate during the birth season and kill unrelated infants (Pereira and Weiss, 1991). *L. catta* male attacks on infants have been observed at one site in the wild, Berenty (Hood, 1994; Jolly et al., 2000; Ichino, 2005), and at one captive location, the Duke Primate Center (Pereira and Weiss, 1991; Jolly et al., 2000).

However, male infant-killing behavior as an adaptive strategy in this species has been questioned for several reasons (see Sauther et al., 1999 and Sussman, 1999), including a conspicuous lack of male infanticidal behavior at sites where *L. catta* have been well-studied for many years (e.g., Beza Mahafaly: Sauther, 1991; Sauther and Sussman, 1993; Gould, 1994; Sauther et al., 1999). Because *L. catta* females in the wild commonly mate with both troop and extra-troop males during estrus (Jolly, 1966; Koyama, 1988; Sauther, 1991; Sussman, 1992; Gould, 1994), males would need to be able to identify their own offspring and only target the offspring of other males for infanticide to be adaptive. Furthermore, because *L. catta* breed seasonally (Jolly, 1984; Rasmussen, 1985), females also would not come into estrus any sooner as a result of infant loss via infanticide. Concerning this last point, Pereira and Weiss (1991) suggest that losing an infant in one year should increase the chances of survival for the infant born to the female in the following year, though this suggested trend of increased infant survival following infant loss has not been demonstrated for any *L. catta* population to date. Infanticide by males was not observed during the course of the present study, and has not been witnessed on St. Catherines Island (Parga and Lessnau, 2005; Lessnau, pers. comm.). Consequently, it does not appear that the inter-troop movement of males during the birth season on St. Catherines is an adaptation to promote infanticide.

Instead, males may frequently transfer into new groups during the birth season on St. Catherines because there is less competition from resident males at this time, as no female is sexually receptive. A case study supporting this idea can be found during the 2003 mating season, when males CP and MX transferred into Group 3 from neighboring Group 2 only after the two adult resident males were enclosed in the group's shelter sites due to injury. These two migrating males were the only males to ever transfer during the first estrus cycle of the mating season at this site (October-November), when rates of aggression among males are extremely high, especially on days of estrus (Parga, 2006). Hence, the birth season may be an optimal time for males to change groups while minimizing the amount of aggression received from resident males of the group they are attempting to join.

Males Transferring Together Versus Alone: Functional Explanations

Males in this study frequently transferred between groups in pairs or triplets. Less than one-quarter of transfers were performed by lone males. Natal males in particular were significantly more likely to transfer between groups with at least one other male than alone. Similarly, wild *L. catta* males often transfer between groups in pairs or triplets (Budnitz and Dainis, 1975; Jones, 1983; Sussman, 1991, 1992; Gould, 1994, 1997), as do males of several other primate species (e.g., Japanese macaques, *Macaca fuscata*: Sugiyama, 1976; long-tailed macaques, *M. fascicularis*: van Nooordwijk and van Schaik, 1985, 2001; rhesus macaques, *M. mulatta*: Drickamer and Vessey, 1973). Transferring with a partner has been identified as a highly adaptive behavior, because a

transfer partner can help provide protection against predators or against aggression from resident individuals of the group into which the males are attempting to migrate (i.e., capuchin monkeys, *Cebus capucinus*: Jack and Fedigan, 2004a; vervet monkeys, *Cercopithecus aethiops*: Cheney, 1983, Cheney and Seyfarth, 1983).

Migrating *L. catta* males in the wild receive aggression from resident individuals in the troop that they are attempting to join; a transfer partner can help males to spot impending attacks from these individuals or from predators (Sussman, 1992; Gould, 1994, 1997). There exist many *L. catta* predators in Madagascar, including aerial predators such as the Madagascar harrier hawk, *Polyboroides radiatus*, and terrestrial carnivores such as the fossa, *Cryptoprocta ferox* (Sauther, 1989). St. Catherines Island additionally has a number of potential lemur predators, including aerial predators such as the red-tailed hawk, *Buteo jamaicensi*s, and the great-horned owl, *Bubo virginianu*s (Parga and Lessnau, 2005). There has also been at least one attack by an alligator on a male *L. catta* on St. Catherines (Keith-Lucas et al., 1999). Therefore, as suggested by Sussman (1992) and Gould (1994, 1997) for wild *L. catta*, transferring with other males on St. Catherines may provide males with a much safer passage than if they were transferring alone.

However, the fact that nearly a quarter of male transfers (most non-natal) on St. Catherines were instances in which males dispersed alone may indicate that males perceive less predation risk (Janson, 1998) on St. Catherines than they would in Madagascar. Predation pressure may be relaxed due to a number of factors, including development on the island (which may decrease the amount of available habitat for

predators), and the prevalent presence of humans on the island (island employees and researchers), especially near the ranging areas of the lemurs.

Also, the sex ratio of *L. catta* groups on St. Catherines often depart from the typical 1:1 ratio (Lessnau, unpub. data) common in the wild (Jolly, 1966; Sussman, 1974, 1991; Mertl-Milhollen et al., 1979). The lemur groups on St. Catherines have more females than males (Table 2.2). In fact, across all years of this study, no more than two to four adult males resided in each of the social groups. Consequently, at any one time, there were only a few male residents which might repel migrating males from social groups. As a result, migrating males on St. Catherines may be more likely to attempt lone transfers than males in the wild because there are fewer resident males per group to direct aggression at them.

Transferring into groups with related males may also be functionally related to kin selection (Meikle and Vessey, 1981). In this study, several groups of males transferring together were related matrilineally. Males frequently transferred out of their natal groups with same-year birth cohort members, or other males born in their natal group who were close in age. Due to female philopatry, all natal males are related. Furthermore, because male mating success suggests that there may be reproductive skew among males in this population (refer to Chapter 2), many cohort members can additionally share the same father, and thus may share an even larger degree of kinship. Some younger natal males may have also transferred out of their natal groups with their fathers, because every male who dispersed from his natal group with at least one other male did so with either a

fellow natal male, or a male who was both old enough to sire him and was in the social group at the time of the male's conception.

Travelling with an older male, regardless of relatedness, may be particularly important for young *L. catta* males, because the experience of the older male can aid the successful integration of the younger male into a new social group (Gould, 1994). A transfer partner (or partners) can provide migrating males with valuable affiliative relationships while they are making the transition from one group to another (Gould, 1994, 1997).

Male Dominance Status and Transfer Behavior

Transferring between social groups is one way that males can improve their dominance status (Pusey and Packer, 1987). Indeed, in some primates, lower-ranking males are more likely to transfer between groups than are higher-ranking males (e.g., vervet monkeys, *Cercopithecus aethiops*: Cheney, 1983). Sussman (1992) suggested that male inter-troop transfers in *L. catta* may be a mechanism by which males increase their status as the "central" highest-ranking (Sauther, 1991) male of the group. Gould (1994) found evidence in support of this hypothesis. Subordinate males on St. Catherines might therefore be expected to transfer more frequently between groups in an attempt to increase their social status. Instead, higher-ranking males more frequently migrated in this study, and lower-ranking males were more likely to remain in their social groups.

One explanation for this trend may be that higher-ranking males were more likely to attempt migrations in the first place, or that higher-ranking males were more successful

at their migration attempts. Because short-term male visits (less than a week in length) were not routinely recorded by WCS staff on St. Catherines, the number of attempts at migration by lower versus higher-ranking males is unknown. Lower-ranking males may have attempted to migrate as frequently as higher-ranking males, but their migration attempts could have failed if they did not remain in these new groups due to the stress of the migration process or due to the aggression directed at them by group residents. Sussman (1991) notes that transferring males appear to experience nutritional stress, as evidenced by low body weight during the migration period. Cortisol measures have also confirmed that male inter-troop migration is a stressful period for *L. catta* males (Pride, 2005). Because male transfer appears to be a difficult process for male *L. catta*, inter-troop migration may be a strategy more frequently used by higher-ranking males.

Also, because male dominance rank does not correlate with male mating success in this *L. catta* population (Chapter 2), high-ranking males may be able to increase their mating success by transferring between groups. Even for a high-ranking male who has high mating success in a current troop, diversifying female mates by transferring groups may be an adaptive strategy, as it would allow for greater genetic diversity among offspring, an explanation frequently given for female multiple mating (Williams, 1975; Gladstone, 1979).

Male Transfer as a Mating Strategy

A. Natal Male Dispersal

On St. Catherines males usually leave their natal troop at the age of two or three years. No male remained in his natal troop longer than three years, with the single exception of one male who was three years, seven months at the time of his group's removal from the population for management purposes. By the time that males migrate into their new social groups on St. Catherines, they are already sexually mature and can take advantage of mating opportunities. Indeed, one yearling male (MX, Table 4.1) was observed to mate with a female to ejaculation following his breeding season migration into this new group. Natal male dispersal therefore appears to be a successful strategy by which *L. catta* males on St. Catherines can increase their mating success early in life. Though young (one to two year old) natal males frequently attempted to mount related estrus females in this study (Parga, unpub. data), no natal male was ever observed to gain penile intromission with a matrilineally-related female. Natal male mount attempts were routinely met with vigorous aggression by the female (Parga, 2002a). Female incest avoidance of this kind has also been found at captive locations (i.e. the Duke University Primate Center: Taylor and Sussman, 1985; Taylor, 1986) and in the wild (Sauther, 1991). In fact, no study of wild *L. catta* sexual behavior has documented the mating of a natal male within his own group (Koyama, 1988; Sauther, 1991; Sussman, 1992; Gould, 1994, 1997). Therefore, because of female incest avoidance, a male's mating opportunities are severely limited within his natal group.

On St. Catherines a natal male's mating opportunities are likely additionally constrained because the extra-troop matings which are common in the wild (Sauther, 1991; Sussman, 1992; Gould, 1994, 1997) have not been observed at this site (Parga, 2002a, pers. obs.), making it even less likely that males will garner any degree of mating success while remaining in their natal groups. Unless natal males on St. Catherines disperse, their mating success is predicted to be virtually non-existent. For this reason, natal male migration can be considered an important mating strategy for *L. catta* males on St. Catherines Island.

Notably, no male ever returned to his natal troop, despite the fact that some males migrated several times during the study period. Similarly, in many other group-living primates with male dispersal, males rarely, if ever, return to their natal groups to breed (baboons, *Papio anubis*, Packer, 1979a; toque macaques, *Macaca sinica*: Dittus, 1979; Japanese macaques, *Macaca fuscata*, Sugiyama, 1976; rhesus macaques, *M. mulatta*: Drickamer and Vessey, 1973). This pattern of avoidance of returning to the natal group is even more striking when one considers the small number of lemur groups on St. Catherines. Throughout much of the colony's history, there have only been three to four social groups (Parga and Lessnau, 2005), resulting in very few options for males attempting to migrate out of their current group. Clearly, males did not randomly select troops into which to migrate, as numerous males would have returned to their natal groups if that were the case. As a consequence, the degree of inbreeding on St. Catherines is probably lower than it otherwise would be due to this trend in male avoidance of the natal troop.

B. Non-Natal Male Dispersal

Lack of mating success in a male's current group is often identified as a potential cause of male emigration in primates (Altmann and Altmann, 1970; Packer, 1979a). This may be a plausible explanation for natal male migration on St. Catherines, but can only partially explain the non-natal male migrations at this site. Although increased mating success following immigration was documented for some males, others leave their social groups following a season in which they have high mating success, and some males with poor mating success remain in their social groups.

An alternate explanation is that adult males may transfer for a second or third time after remaining in a non-natal troop for a period of years (even following a mating season in which they show high mating success) because such a strategy is highly adaptive from the perspective of offspring genetic variability. Even for males showing moderate to high degrees of mating success in their groups, migration to new groups would provide the opportunity to mate with new females, and would allow males to increase the overall genetic diversity of their offspring (Williams, 1975; Gladstone, 1979).

Also, because females on St. Catherines have shown sexual preference for novel males (Chapter 4; Parga, 2002a), males may do better to transfer into a new group to take advantage of their novelty status, a trend which has been documented in Japanese macaques, *Macaca fuscata*, where female choice for novel males has been found (Huffman, 1991). Even if a male's current mating success is high in a particular group, migrating may be a successful strategy to offset future declines in mating success.

Number of Non-Natal Males Per Group Determines Male Migration Patterns

It might be expected that males would transfer into groups in which greater numbers of mates are available, or in which the sex ratio is more skewed towards females than in the groups from which they came (e.g., rhesus macaque, *Macaca mulatta*: Drickamer and Vessey, 1973; baboon, *Papio anubis*: Packer, 1979a). Among wild *L. catta* males at Beza Mahafaly, one study showed that males were more likely to leave groups with higher male-to-female sex ratios (Sussman, 1991). However, among males on St. Catherines there was no significant difference between pre- and post-migration groups in the numbers of females per group or in the group sex ratio. Males belonging to groups having sex ratios with more males to females were no more likely to migrate out than they were to remain in their social groups.

Instead, the number of males per group appeared to strongly determine male migration decisions. Males on St. Catherines were significantly more likely to join a group with fewer non-natal males than the group that they left. This trend was noted for wild *L. catta* males at Berenty, and was interpreted as male avoidance of groups with a greater number of potential competitors (Jones, 1983). However, male *L. catta* in the wild do not universally migrate into groups with fewer males. For example, Gould (1994) found that only in four of ten instances of migration did males at Beza Mahafaly migrate into groups having fewer males than in their groups of origin.

Male Dispersal in Captive or Novel Environments

In an age where the future stability and survival of many wild primate populations is tenuous (Chapman and Peres, 2001) and conservation is of primary importance in both captive and wild settings (Feistner and Price, 2002), the establishment of primate colonies in novel environments may be one potential way to circumvent primate species loss. The transportation and release of primates in non-endemic areas can be a fruitful area of conservation work.

The potential for inbreeding depression is a major concern in any managed primate population, and animal husbandry personnel often must make difficult decisions concerning the addition or removal of individuals from groups or populations (Pfeifer, 1996). If animal movement between social groups is facilitated, animals may choose to disperse of their own volition and aid outbreeding, even in a captive setting where options are limited. For example, at the Duke University Primate Center (DUPC) where primates semi-free range in large tracts of enclosed forest (Bergeron, 1974), adjoining ruffed lemur (*Varecia variegata*) males transferred between groups and mated with females in the new group when fences separating groups were removed (White et al., 1993). Hence, although every managed primate colony will require some level of human involvement, if opportunities for male dispersal exist there may be gene flow provided for by the animals themselves, without the need for human intervention.

CONCLUSIONS

There are few opportunities for male inter-group transfer on St. Catherines Island due to the small size of the colony and small number of social groups. Nevertheless, males migrate frequently between social groups. In fact, males migrate on average about every 3.2 years, which is similar to the frequency of male migration in Madagascar, which occurs every 3.5 years on average. Males also remain in social groups for about as long as males in the wild (mean troop tenure length is 2.2 years on St. Catherines and 2.8 years in Beza Mahafaly, Madagascar). Male transfer shows the same seasonal pattern as that which occurs in Madagascar. Most transfers on St. Catherines occur around the birth and lactation seasons, with a handful occurring during the breeding season. The main difference in male transfer behavior between the two locations is earlier natal migration on St. Catherines. This difference may be due to food provisioning causing the early sexual maturation of males, or by the female-biased sex ratio on St. Catherines, which results in fewer resident males per social group to repel potential immigrants.

Dominant males appear to transfer out of social groups more frequently than lower-ranking males, which may indicate that higher-ranking males can more easily endure the difficulty of inter-troop migration than lower-ranking males. Dominant males may also be more willing to attempt transfers, or their transfer attempts may simply be more successful than migration attempts by lower-ranking males.

Male inter-troop transfer has been identified as a potential male mating strategy in some primates (e.g., capuchin monkeys, *Cebus capucinus*: Jack and Fedigan, 2004b; vervet monkeys, *Cercopithecus aethiops*: Henzi and Lucas, 1980), including wild *L. catta*

(Sauther, 1991; Sauther and Sussman, 1993; Sussman, 1999). Inter-group migration among males on St. Catherines Island can also be considered a mating strategy, as males can sometimes markedly increase their mating success by transferring into a new social group. At this site, females show a preference for novel males as mates (Chapter 5), and some males showed increased mating success during their first breeding season in a new social group as compared with their previous mating success in their old group. However, the relationship between male mating success and inter-troop transfer is highly specific to the individual. Sometimes males with poor mating success will remain in groups for more than one season (MC, Table 4.3), and sometimes males with high mating success will choose to leave (ED in 2000, Table 4.3).

The number of males in a prospective group appears to be a critical variable in male *L. catta* transfer decisions on St. Catherines. Though there were no significant differences in the number of reproductively-mature females or in the group sex ratio between pre-and post-migration groups of residence, males in this study were significantly more likely to join a group with fewer males than the group from which they came. This pattern underscores the importance of male dispersal as a mating strategy, as male avoidance of groups with larger numbers of males might indicate that males bypass groups in which they would be forced to compete with a greater number of males during intra-sexual mating competition during the breeding season.

Finally, it is notable that no male ever returned to his natal group, despite frequent transfers throughout the lifetime of a male. This avoidance of returning to the natal group likely decreases incest, as might subsequent male inter-group transfers that take place

every few years on average following a male's initial natal migration. In closing, St. Catherines Island aptly serves as a model for other non-endemic primate colonies by providing evidence that, if given the opportunity, individuals can cause gene flow by exhibiting natural migration patterns in a novel setting.

Table 4.1: List of natal male transfers

Male	Date of transfer	Age at 1st transfer (yrs)	# of individuals with whom this male transferred	Identity of male transfer partner(s)	Was the transfer partner a cohort member?	Was the transfer partner a natal male?	Group of origin	Group migrated into	# of female mates in new group
EK	02-May-00	2.1	0	None	-	-	3	1	1(.25)
BY	01-Aug-97	2.3	Unknown*	Unknown*	Unknown*	Unknown*	2	3	Unknown*
MN	08-Apr-01	2.1	1	KL	No	No	2	3	3(.75)
BR	05-Apr-01	3.0	1	Subadult male	No	Yes	3	2	Unknown*
JH	02-Mar-00	2.8	0	None	-	-	3	2	Unknown*
RY	24-Jun-01	2.3	1	CH	Yes	Yes	3	2	Unknown*
CH	24-Jun-01	1.9	1	RY	Yes	Yes	3	2	Unknown*
DA	01-Mar-02	1.9	1	LE	Yes	Yes	3	4	Unknown*
LE	01-Mar-02	1.9	1	DA	Yes	Yes	3	4	Unknown*
CL	05-Apr-03	3.0	1	RI	No	Yes	4	Ranging**	None
CP	05-Nov-03	2.6	1	MX	No	Yes	2	3	7(.7)
WD	05-May-03	2.1	1	BY	No	No	3	Ranging**	None
RI	05-Apr-03	1.9	1	CL	No	Yes	4	Ranging**	None
TD	31-Mar-05	2.0	1	GA	Yes	Yes	4	2	Unknown*
GA	31-Mar-05	2.0	1	TD	Yes	Yes	4	2	Unknown*
MX	05-Nov-03	1.6	1	CP	No	Yes	2	3	4(.4)
FZ	02-Mar-04	1.8	2	BR,ED	No	No	2	4	1(.25)

* Not recorded in WCS records, and this study did not encompass this information

** These males transferred to a part of the island where no free-ranging lemur groups reside

Note: The column entitled "Number of female mates in a new group" lists both the absolute number of females a male was observed mounting as well as the percentage of females that that number stands for (out of the total number of females observed in estrus).

Table 4.2: List of non-natal male transfers

Male	Date of transfer	Duration of troop tenure prior to dispersal (yrs)	# of individuals with whom this male transferred	Age at this transfer (yrs)	Identity of male transfer partner(s)	Group of origin	Group migrated into	# of female mates in old group	# of female mates in new group
KL	19-Jul-98	Unknown*	1	5.3	MK	3	2	Unknown**	Unknown**
KL	08-Apr-01	2.7	1	8.1	MN	2	3	Unknown**	4(1.0)
KL	30-Mar-05	4.1	0	12.0	None	3	2	1(.5)	Unknown**
KL	23-Apr-05	0.1	0	12.1	None	2	4	Unknown**	Unknown**
MK	19-Jul-98	4.3	1	11.2	KL	3	2	Unknown**	Unknown**
BY	05-May-03	5.8	1	8.1	WD	3	Ranging***	2(1.0)	None
ED	26-Jan-01	Unknown*	0	9.9	None	3	2	4(.8)	Unknown**
ED	02-Mar-04	3.1	2	13.0	BR,FZ	2	4	1(.33)	3(.75)
BR	02-Mar-04	2.9	2	6.0	ED,FZ	2	4	1(.33)	2(.5)
LE	22-Apr-03	1.1	0	3.1	None	4	2	Unknown**	3(1.0)
JH	11-Apr-00	0.1	0	3.0	None	2	4	Unknown**	Unknown**
TD	09-May-05	0.1	1	2.1	GA	2	Ranging***	None	None
GA	09-May-05	0.1	1	2.2	TD	2	Ranging***	None	None

* This male's troop tenure began prior to WCS personnel collecting data on troop composition

** Not recorded in WCS records, and this study did not encompass this information

*** These males transferred to a part of the island where no free-ranging lemur groups reside

Note: The columns entitled "Number of female mates in a new/old group" list both the absolute number of females a male was observed mounting as well as the percentage of females that that number stands for (out of the total number of females observed in estrus).

Table 4.3: Male mating success, transfer behavior and group sex ratios

Male	Breeding year	Group	# females mated	# females obs in estrus	% females mated	Did male migrate or stay after this season?	Group sex ratio (M/F)
EK	2000	1	1	4	0.25	Stayed	0.8
EK	2001	1	2	2	1	Stayed	0.43
FD	2000	1	1	4	0.25	Stayed	0.8
FD	2001	1	2	2	1	Stayed	0.43
SP	2000	1	1	4	0.25	Stayed	0.8
SP	2001	1	2	2	1	Stayed	0.43
RK	2000	1	3	4	0.75	Stayed	0.8
KL	2001	3	4	4	1	Stayed	0.67
KL	2002	3	2	2	1	Stayed	0.25
KL	2003	3	2	10	0.2	Stayed	0.4
KL	2004	3	1	2	0.5	Migrated	0.33
MN	2001	3	3	4	0.75	Stayed	0.67
MN	2002	3	2	2	1	Stayed	0.25
MN	2003	3	2	10	0.2	Stayed	0.4
MN	2004	3	2	2	1	Stayed	0.33
BY	2000	3	3	5	0.6	Stayed	0.67
BY	2001	3	2	4	0.5	Stayed	0.67
BY	2002	3	2	2	1	Migrated	0.38
ED	2000	3	4	5	0.8	Migrated	0.5
ED	2002	2	3	5	0.6	Stayed	0.8
ED	2003	2	1	3	0.33	Migrated	0.8
ED	2004	4	3	4	0.75	Stayed	0.67
BR	2002	2	3	5	0.6	Stayed	0.8
BR	2003	2	1	3	0.33	Migrated	0.8
BR	2004	4	2	4	0.5	Stayed	0.5
MC	2000	3	0	5	0	Stayed	0.67
MC	2001	3	1	4	0.25	Stayed	0.67
CH	2002	2	5	5	1	N/A*	N/A*
RY	2002	2	5	5	1	Stayed	0.8
RY	2003	2	2	3	0.67	Stayed	0.4
DA	2004	4	2	4	0.5	Stayed	0.5
LE	2003	2	3	3	1	Stayed	0.4
CP	2003	3	7	10	0.7	N/A*	N/A*
MX	2003	3	4	10	0.4	N/A*	N/A*
FZ	2004	4	1	4	0.25	N/A*	N/A*

* These males were removed for management purposes or due to injury prior to their potential migration

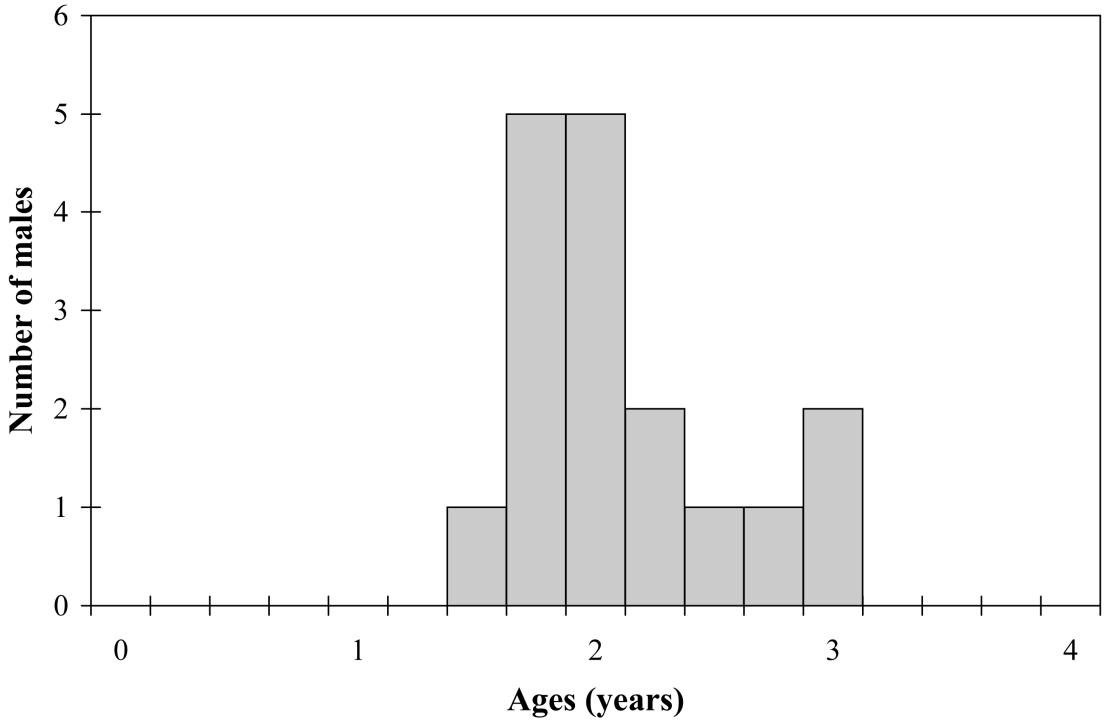

Figure 4.1: Natal migration on St. Catherines Island by male age. This histogram shows the number of males which transferred at each age from their natal groups on St. Catherines Island (n = 17).

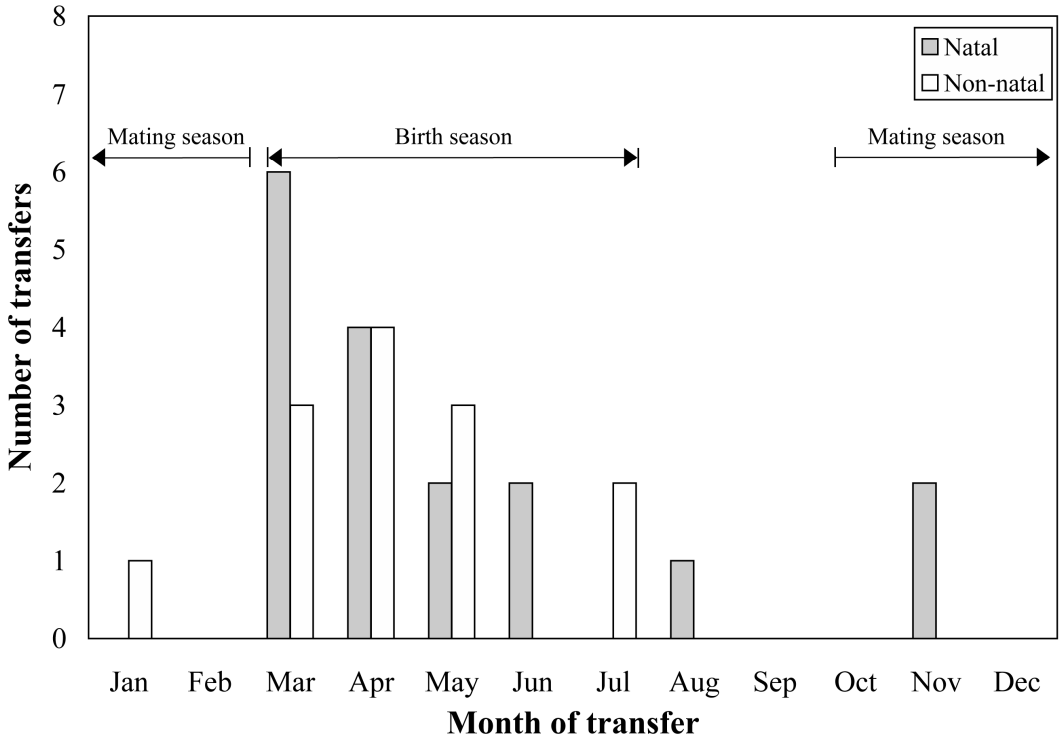

Figure 4.2: Seasonality of male inter-troop transfer on St. Catherines Island. This histogram shows the seasonality of both male natal (n = 17) and non-natal (n = 13) transfers on St. Catherines between 1997-2005.

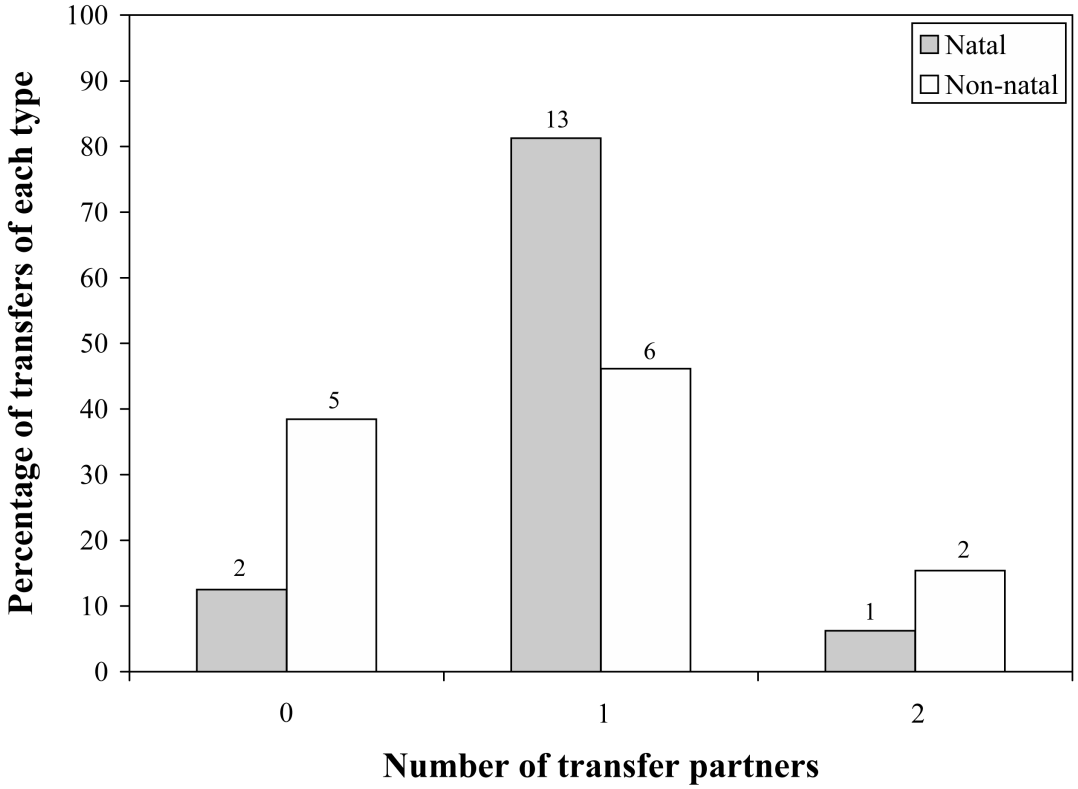

Figure 4.3: Number of inter-troop transfer partners for natal and non-natal males. Males performing natal transfers are most likely to be accompanied by one transfer partner than either transferring alone or with two partners (Chi-square goodness of fit: $\chi^2 = 16.63$, df = 2, $p < 0.0003$). In contrast, males performing non-natal transfers are equally likely to transfer alone or with other males (Chi-square goodness of fit: $\chi^2 = 2.00$, df = 2, $p < 0.368$, NS). The number of transfers are listed above each bar.

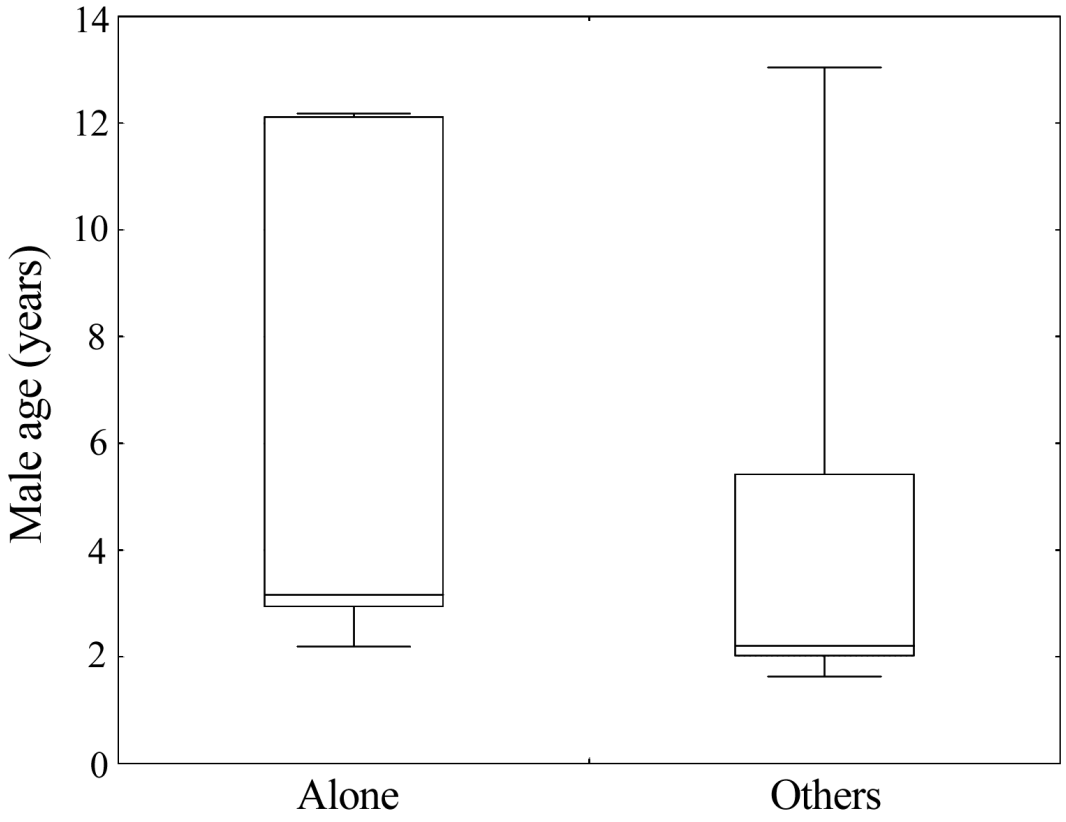

Figure 4.4: Males transferring alone or with others by age. Male age did not affect whether males transferred alone or with other males (Kolmogorov-Smirnov: $n_1 = 7$, $n_2 = 22$, $p > 0.10$, NS). Boxes represent interquartile range, whiskers represent maximum and minimum values, and lines represent median values.

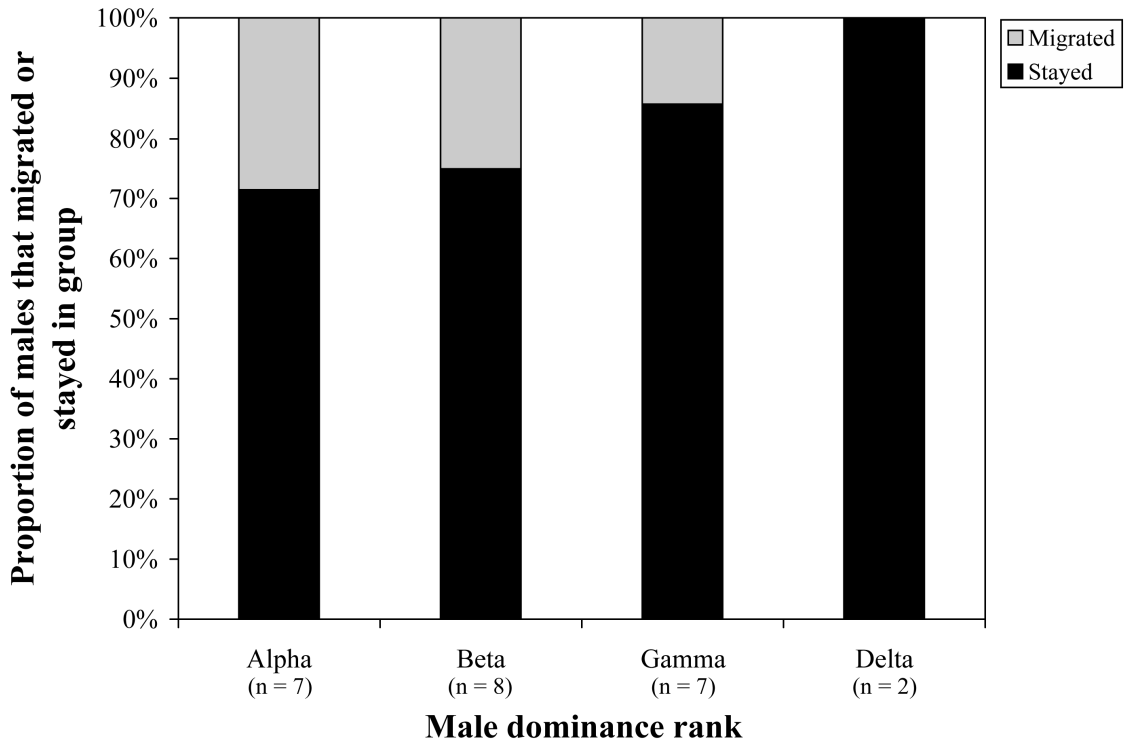

Figure 4.5: Proportion of males remaining in their groups by dominance rank. Higher-ranking males are significantly more likely to migrate out of a social group than are lower-ranking males (Friedman's 2-way ANOVA: $\chi^2 = 4.00$, df = 1, $p < 0.046$).

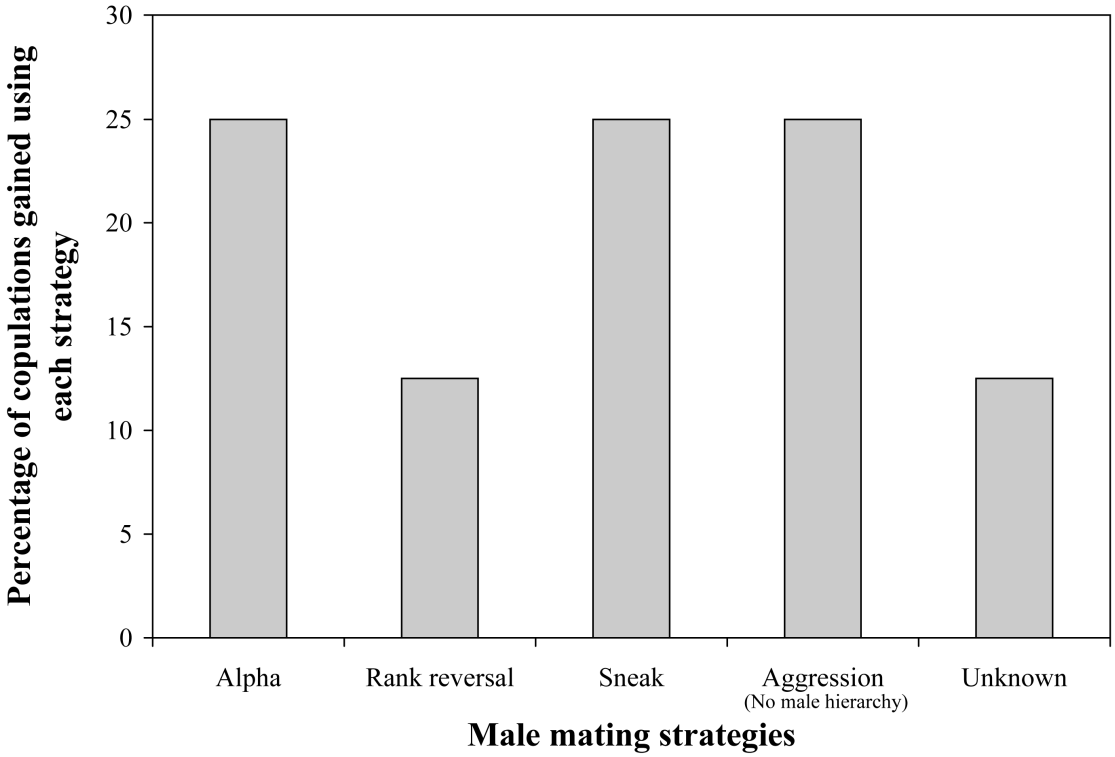

Figure 4.6: Male mating strategies used in the first mating season following a male's transfer from his natal group. Males were no more likely to use aggressive (alpha, rank reversal, aggression with no male dominance hierarchy) versus non-aggressive strategies such as sneak copulation (Chi-square goodness of fit test: $\chi^2 = 2.57$, df = 1, n = 16, $p < 0.109$, NS)

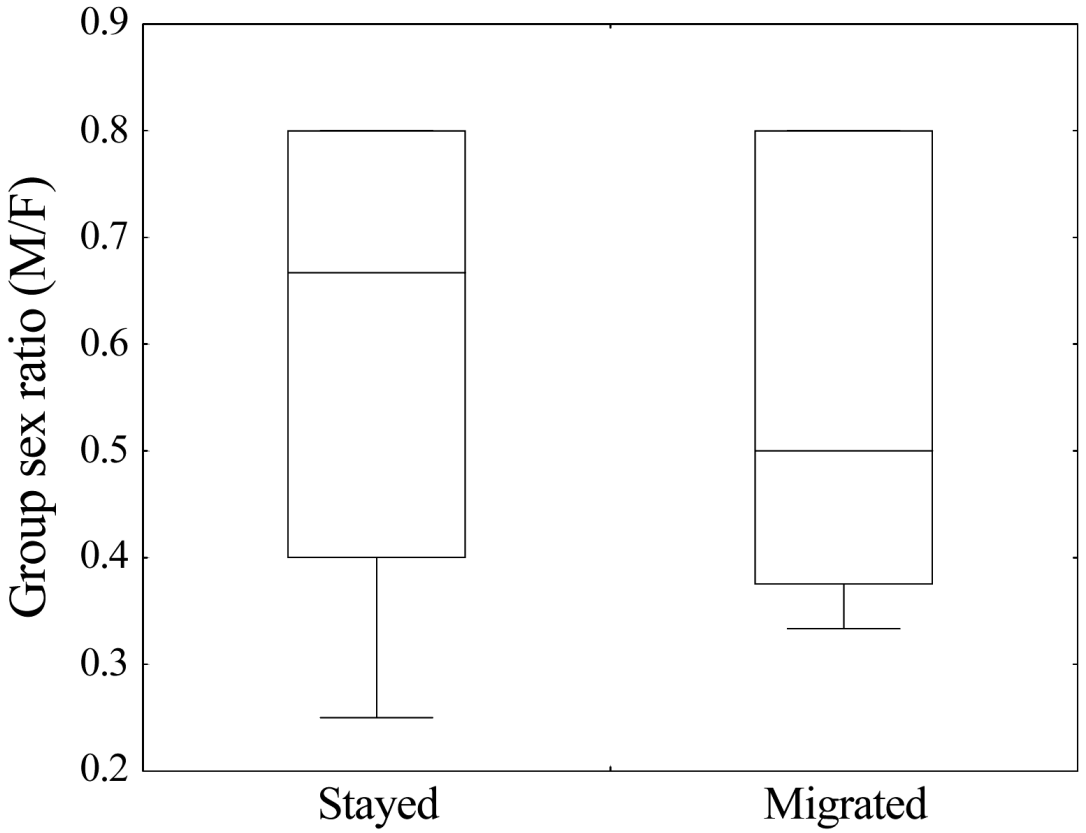

Figure 4.7: Males who stayed or migrated based on group sex ratio. Males who remained in their social groups were no more likely to come from groups with more favorable sex ratios (fewer males per female) than were males who migrated (Kolmogorov-Smirnov: $n_1 = 5$, $n_2 = 26$, $p > 0.10$, NS). Sex ratios were calculated based upon the number of non-natal males in a social group, and the number of females aged 2 years and older. Boxes represent interquartile range, whiskers represent maximum and minimum values, and lines represent median values.

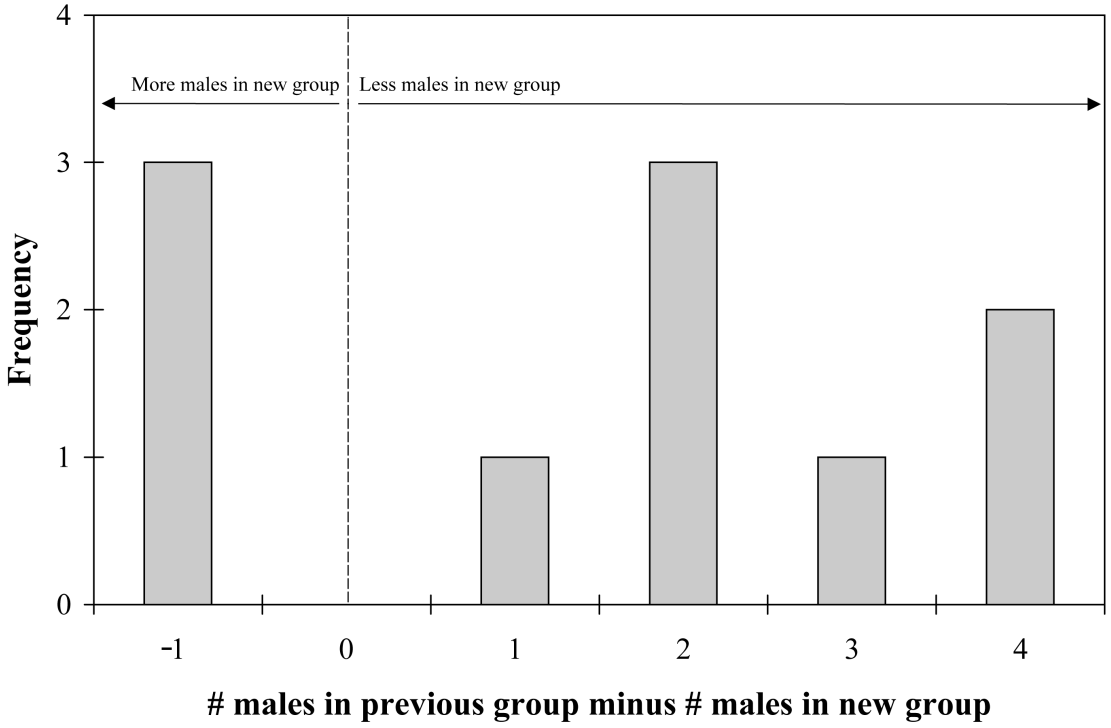

Figure 4.8: A comparison of the number of males within a male's pre- and post-transfer group. Males were significantly more likely to transfer to a group with fewer non-natal males than the group which they left (Wilcoxon: $Z = 2.04$, $n = 10$, $p < 0.042$).

CHAPTER 5: FEMALE MATE CHOICE

INTRODUCTION

The Female Mate Choice Component of Sexual Selection

There has been a long history of interest in the topic of female mate choice in primatology, although the evidence for female mate choice has been questioned at times, as has its evolutionary importance. Whereas some researchers have suggested that the evidence for female mate choice in non-human primates is weak or modest at best (Keddy-Hector, 1992), others have highlighted the marked effects female choice can have on male mating success (Schurmann and van Hooff, 1986).

Sexual selection theory predicts that females should be highly selective with respect to potential mates because females have greater parental investment than do males (Trivers, 1972). Consequently, females are expected to have evolved mechanisms by which they can evaluate among several potential mates and identify the best male or males (Janetos, 1980). Females are expected to choose males who can best provide them and/or their offspring with direct benefits such as food (Tutin, 1979) and parental care (van Schaik and Paul, 1996), or indirect (genetic) benefits (Andersson, 1994). Genetic benefits may accrue to females who select mates based upon genetic complementarity (Penn, 2002) or upon male genetic quality, which is often termed "good genes" (Paul, 2002).

Traits which have been identified as potential indicators of male quality in animals include the roaring vocalizations of male red deer, *Cervus elaphus* (Clutton-

Brock and Albon, 1979), the bright plumage indicative of parasite resistance in birds (Hamilton and Zuk, 1982), and more recently studied, the red facial characteristics of male rhesus macaques, *Macaca mulatta* (Waitt et al., 2003). Such "honest indicator" traits would be expected to be targets of female sexual preference, as they are thought to provide a true indication of a male's genetic quality. In primates, physical traits have been identified as being potentially less important in mate choice than among other animal species (Setchell and Kappeler, 2003). Instead, social traits such as male dominance status appear to be important in primate female mate choice decisions (Small, 1989).

Male dominance status has long been thought to signal genetic quality among animals (Cox and Le Boeuf, 1977). If dominance status is an accurate indication of male quality in primates, one expectation is that females would sexually prefer the most dominant male or males in a group. As might be expected, female primates of many species prefer to mate with dominant males (capuchins, *Cebus apella*: Janson, 1984; Welker et al., 1990; Phillips et al., 1994; Linn et al., 1995; Lynch, 2001; chimpanzees, *Pan troglodytes*: Matsumoto-Oda, 1999; howler monkeys, *Alouatta palliata*: Jones, 1985; golden lion tamarins, *Leontopithecus rosalia*: Baker et al., 1993; vervet monkeys, *Cercopithecus aethiops*: Keddy, 1986; sifaka, *Propithecus verreauxi*: Brockman, 1999).

A non-mutually exclusive hypothesis is that female primates should show sexual preference for novel or unfamiliar males as an inbreeding avoidance mechanism. Female preference for novel males has been well documented in such species as Japanese macaques, *Macaca fuscata* (Huffman, 1991; Takahata et al, 1999), rhesus macaques, *M.*

mulatta (Bercovitch, 1997), and olive baboons, *Papio cynocephalus* (Packer, 1979a). Unfortunately, however, the male characteristics most highly preferred by female primates are often difficult to identify, especially because substantial methodological difficulties can be encountered when studying female mate choice.

Studying Female Mate Choice in Primatology: Challenges to Measuring Female Sexual Preference Accurately

One confounding factor plaguing studies of female mate choice is that female mating behavior, as measured by researchers, may not accurately portray true female sexual preferences. As succinctly put by Fedigan (1982), is it, "female choice, or Hobson's choice?" (p. 269) suggesting that females may not be mating with highly sexually preferred males, but may instead be lacking any better alternative. Indeed, part of the difficulty in documenting mate choice is that in many species, female sexual preference cannot be easily measured due to male tactics that preclude a female from gaining access to certain males due to male-male competition (Kuester and Paul, 1992) or male sexual coercion. Male sexual coercion can take the form of male forced copulation of females, or male abuse of females in a sexual context (Smuts and Smuts, 1993). For example, rhesus macaque (*Macaca mulatta*) females can sometimes be the target of male aggression simply by being in proximity to lower-ranking males (Manson, 1992, 1994). Another potential problem in mate choice studies is that female mating preferences can be masked by male mating competition if researchers focus on the more salient behaviors

of male aggression and overlook more subtle female behaviors which suggest differential female sexual preference among prospective mates (Halliday, 1983).

The majority of shortcomings in studies of mate choice are often due to male control of mating situations and/or harassment of females (Clutton-Brock and Parker, 1989). Such male behaviors are especially prevalent in species where males are dominant over females. Therefore, for the present study of female mate choice, a female dominant (Richard, 1987) primate species was selected. Due to female dominance, the factors which commonly confound mate choice studies (i.e., male harassment of females) were expected to be absent, allowing for a closer approximation of true female sexual preferences. Females in such species would likely have more freedom to exhibit sexual preferences than females in male dominated primate groups.

The ring-tailed lemur (*Lemur catta*) is often regarded as a quintessentially female dominant species, in which all reproductively mature females are consistently able to agonistically dominate troop males (Jolly, 1966, 1984; Budnitz and Dainis, 1975; Taylor and Sussman, 1985; Taylor, 1986; Kappeler, 1990a, 1993a; Pereira et al., 1990; Sauther, 1992; Gould, 1994; Nakamichi and Koyama, 1997; Pereira and Kappeler, 1997; Sauther et al., 1999). Some researchers have even hypothesized that females have free choice of mates in female dominant species (Pereira and Weiss, 1991). Hence, this species was chosen for a multi-year study of female mate choice.

Reproduction in *L. catta*

L. catta, like most Malagasy primates, breed seasonally (Jolly, 1984; Rasmussen, 1985). Because females are only sexually receptive during the peri-ovulatory period (also known as vaginal estrus: Evans and Goy, 1968; Van Horn and Resko, 1977), all copulations are potentially conceptive. There are no non-conceptive matings in this species, such as that which occurs in anthropoids (e.g. Manson et al., 1997). Each female's estrus period lasts for approximately a day or less (Jolly, 1966; Evans and Goy 1968; Van Horn and Resko 1977), and the entire estrus period can be as short as three and a half hours (Koyama, 1988; Sauther, 1991; Parga, 2006). A single copulatory event can contain several separate mounts (some with and some without intromission) before ejaculation is achieved, and males only ejaculate once with a female during a single estrus period (Sauther, 1991; Parga, 2003; Parga et al., 2006). *L. catta* can therefore be placed in category #10 (no copulatory lock, thrusting, multiple intromissions, single ejaculation) according to the schema devised by Dewsbury (1972) to describe mammalian mating patterns.

Females within a social group will cycle within one to three weeks of one another (Sauther, 1991). Captive studies indicate that female *L. catta* can cycle up to three times per season if kept under natural light conditions, with each cycle being separated by an average of 39 days (Evans and Goy, 1968). Though females can cycle three times per year, most females who conceive do so during their first estrus cycle of the season (Sauther, 1991; Parga and Lessnau, 2005). Females also experience asynchronous estrus (Pereira, 1991; Sauther, 1991).

Previous studies of *L. catta* mating behavior in captivity and the wild have shown that females frequently mate with more than one male during a single estrus period (Taylor 1986; Koyama 1988; Pereira and Weiss 1991; Sauther 1991; Sussman 1992; Sauther and Sussman 1993; Gould 1994, 1996). However, no study has documented female multiple mating or female mate choice in this species over a multi-year period. Until this project, only short-term studies of *L. catta* mating behavior had been conducted, across one to two breeding seasons: two on semi-free-ranging *L. catta* groups at the Duke University Primate Center (Pereira and Weiss, 1991; Cavigelli and Pereira, 2000), and in the wild, by Jolly (1966), Koyama (1988), Sauther (1991), Gould (1994, 1996) and Gould et al. (2005).

Female Mate Choice in *L. catta*

Previous *L. catta* studies have shown variability with respect to the male traits most commonly preferred by females (Sauther et al., 1999). In Beza Mahafaly, Madagascar, Sauther (1991) and Sauther and Sussman (1993) found that females often selectively mated first with the troop's high-ranking males, followed by extra-group males. Koyama (1988) in Berenty, Madagascar, likewise noted that females mated first with high-ranking males, followed by lower-ranking troop males. Although based on these studies high male dominance rank and extra-group status appear to be preferred male traits, high-ranking males are not always the first to mate in the wild; females also frequently mate with lower-ranking subordinate males as well as extra-troop males (Jolly, 1966; Budnitz and Dainis, 1975; Sauther, 1991; Sussman, 1992; Gould, 1994, 1996).

Taylor (1986) and Taylor and Sussman (1985) documented female avoidance of mating with matrilineally-related males in captivity, a behavior also observed among *L. catta* in the wild (Sauther, 1991) and on St. Catherines Island (Parga, 2002a). Hence, previous studies have found multiple mating among *L. catta* females, and a fair amount of variability in female mate choice preferences.

This Study: Testing Hypotheses for Female Mate Choice and Quantifying Female Multiple Mating

For the present project, female mate choice in *L. catta* was revisited in a multi-year study conducted on St. Catherines Island, USA to: 1) identify which male traits appeared to be important in female mate choice, and 2) quantify the extent of female multiple mating in this species. Sauther (1991) previously determined that male mate guarding occurs in this species, a behavior that can potentially constrain female behavior (e.g. mouse lemur, *Microcebus murinus*: Eberle and Kappeler, 2004a). Although males can constrain female mating behavior in this species via mate guarding to a degree, extensive constraint of female mating behavior was not expected. For example, forms of sexual coercion, i.e. forced copulation or male abuse of females (Smuts and Smuts, 1993), were expected to be absent in a female dominant species such as *L. catta*.

Three distinct hypotheses were tested in this study concerning male characteristics that have been shown to be important in studies of female mate choice in non-human primates (see reviews by Keddy-Hector (1992), Small (1989), and Manson (2007)):

Hypothesis 1: Females will prefer males of high dominance status. One commonly-held view is that high male dominance rank is an honest indicator of male quality, representing "good genes" (Andersson, 1994). If male dominance status does indicate quality, then females would be expected to have evolved mating preferences for males exhibiting social traits thought to be associated with male quality, such as high dominance status. The corresponding prediction is that females would preferentially mate with, or sexually present to, the highest-ranked male (or males) in a group.

Hypothesis 2: Among unrelated males, females will prefer older males over younger males. As suggested by Manning (1985), surviving to old age may be an honest indicator of male quality, as reaching old age presumably attests to a male's superior fitness. The corresponding prediction is that females in this study would preferentially mate with, or sexually present to, older group males.

Hypothesis 3: Females will prefer more novel males to more familiar males. Novelty is a characteristic favored sexually by females of many primate species (Small, 1989). If a male is novel and unknown to a female, he is likely unrelated to her. Accordingly, sexual preference for novel males may serve as an inbreeding avoidance mechanism (Packer, 1979a). The corresponding prediction is that females would preferentially mate with, or sexually present to, males with shorter group tenure, and/or the most novel male (or males) in a group.

METHODS

Study Site and Study Animals

Provisioned, free-ranging *L. catta* groups have been maintained on St. Catherines Island, Georgia, USA (Thomas et al., 1978; Thomas, 1988) by the Wildlife Conservation Society since 1985 (Keith-Lucas et al., 1999). This site (located at 31º 40' N latitude, 80º 41' W longitude) is a privately-owned, largely undeveloped semi-tropical barrier island measuring 2,900 hectares, with a mixture of habitats, including pine, oak and palmetto forests, and open pastures as well as savanna and marsh (Keith-Lucas et al., 1999).

Keith-Lucas et al. (1999) provide a brief history of the *L. catta* colony on St. Catherines Island, including a description of lemur behavior following their initial release. The lemurs on St. Catherines are provisioned daily with food (a mixture of monkey chow and fruits and/or vegetables), and water. The lemurs also forage on naturally-occurring vegetation, show ranging behaviors, and have established home range areas (Dierenfeld and McCann, 1999; Keith-Lucas et al., 1999). All adult lemurs have been fitted with uniquely-colored Telonics radio collars (Mesa, AZ). Subadults and small adults were often fitted with nylon collars. Differences in physical characteristics and shaving patterns were used to identify uncollared animals.

At one time, the *L. catta* colony on St. Catherines grew to over 75 individuals in four free-ranging groups (Parga and Lessnau, 2005). Each of these groups was studied across the duration of this project, though different groups were studied in each year. Table 2.1 shows the groups that were studied during the start and middle of the breeding season in each year of this project (spanning late October-December). Table 2.2 shows

the composition of each study group in early October (prior to the start of the mating season) of each year. Each lemur group had between 5-11 females one year of age or older, and 2-4 non-natal males one year of age or older (Table 2.2).

Data Collection on Mating and Social Behavior

A. Breeding Season

Due to photoperiodic regulation, reproduction in *L. catta* on St. Catherines Island is approximately six months out-of-phase with the timing of these events in Madagascar, the endemic habitat of *L. catta* (Rasmussen, 1985). Mating behavior is limited to the fall and winter months (September-February) in the northern hemisphere if the lemurs are exposed to natural light (Evans and Goy, 1968; Van Horn, 1975). Data on mating behavior were collected during five consecutive breeding seasons: October-December 2000-2004, with additional data collected on mating behavior late in the breeding season of one year, during January-February 2004.

During breeding periods, data were collected daily from "dawn to dusk" using 'all-occurrences' sampling (Altmann, 1974) of agonism and reproductive behavior. In mating contexts, the following behaviors were recorded (in addition to recording the agonistic behaviors listed in section "B. Non-Breeding Season" below): jump-fights, mounts, thrusting, and female sexual presents. If observable, penile intromission, ejaculation, and copulatory plug displacement (Parga, 2003) were also recorded, though observation conditions did not always allow these more detailed sexual behaviors to be verified. Ejaculation was indicated by the presence of semen in the female's peri-vaginal

area, and/or on the tip of the male's penis. The start time (and stop time, if appropriate) of each behavior was recorded in seconds. Behavioral estrus was indicated by proceptive (sexual solicitation) or receptive (allowance of male mounting) behavior (Beach, 1976).

During the 2001 through 2004 breeding seasons, one to two field assistants helped monitor groups for estrus behavior and collect social and reproductive data. One observer was stationed per group unless a female was in estrus in one of the groups, in which case two observers paired up at the group with the estrus female.

B. Non-Breeding Season

During the pre-breeding months of each year (June-September in 2000 and 2004, and September-October 2001–2003), data on social behavior were collected approximately five days per week between the hours of 0600 and 1900, with the majority of samples collected between 0800 and 1600. Information on dominance relationships among males was gathered during this time via two main sampling techniques: continuous-time focal animal sampling, and 'all-occurrences' sampling for agonism (Altmann, 1974). Each sampling technique was performed separately, alternating between the two sampling types throughout the day. Each type of sample lasted for 20 minutes during 2000-2001, and was thereafter shortened to 15 minutes in duration. Focal sampling order was randomized, with no more than two samples per individual per day.

During focal samples, the following 'state' behaviors (Martin and Bateson, 1986) were recorded to the nearest second: rest, travel, feed, auto-groom, and allo-groom. The following 'event' behaviors (Martin and Bateson, 1986) were scored: approach, defecate,

urinate, scent-mark (ano-genital, palmar, shoulder, tail), approach-withdraw, bite, chase, cuff, fight, grapple, lunge, nose-push, push, stink-fights, and take food (Jolly, 1966; Petter and Charles-Dominique, 1979; Taylor, 1986; Gould, 1994; Pereira and Kappeler, 1997; Parga, 2002a). *Ad libitum* data were collected at all times during all seasons of the year in both non-mating and mating periods to record sporadic or infrequent events such as predation attempts on the lemurs, instances of mobbing, and alarm or howling vocalizations.

Definitions of Mating, Male Mating Success, Female Mate Choice, and Novelty

Mating is defined as a male mounting a female. A more detailed definition such as 'mounting with penile intromission' or 'mounting with ejaculation' was not used because observation conditions did not always permit documentation of penile intromission or ejaculation during mounts. Male mating success is defined as the number of females a male was observed mounting in a single mating season. Though male reproductive success (number of offspring sired) would be a more desirable measure, paternity data are not available at the present, limiting this analysis to male mating success.

Female mate choice has been previously defined in *L. catta* as a female showing sexual preference for certain males while rejecting others (Sauther, 1991). The definition of female mate choice used in this study differs from that used by Sauther (1991). In the present study, females were considered to exhibit mate choice when they showed *receptivity*, allowance of male sexual advances, or *proceptivity*, sexual solicitation in the

form of sexual presentations, to a male (Beach, 1976). Mate choice was therefore measured as the overall number (and proportion) of group females observed in estrus per season which exhibited proceptive and/or receptive behavior to a male. Rejection of some males was not considered a necessary element of mate choice because in cases in which all non-natal males are deemed sexually acceptable by the female, the absence of a male with whom the female does not want to mate would mean that no mate choice would be scored.

Additionally, some researchers do not consider female receptive behavior as mate choice (and only consider female proceptive behavior as indicating mate choice). However, because this species is female dominant, receptive behavior in this species is not expected to be exhibited unless a male is sexually preferred. In male dominant primate species, there is the possibility that females may show receptivity or acquiescence solely because they are being sexually coerced by a male. For example, in chimpanzees (*Pan troglodytes*), females that are unwilling to accompany a male on a sexual consortship can be coerced to do so by male aggression (Goodall, 1986). In contrast, receptivity in *L. catta* was expected to indicate female sexual preference, because males were expected to be unable to sexually coerce females (but see Chapter 6). Therefore, both receptivity and proceptivity were considered indicative of female sexual preference and mate choice among *L. catta* females.

The definition of male novelty used in this study differs from that used in other studies. Rather than referring to a male who temporarily visits a troop and mates with an estrus female, in the present chapter, novel males are those who migrate into a group but

have not resided in the group as long as other resident males. For example, birth season immigrants (Chapter 3) are considered novel when compared to resident males that have been in the group for a year or more. However, birth season immigrants are considered resident if they have been in the group for several months, and other more novel males have transferred into the group within a month's time or less. Therefore, a male's status as a familiar or novel male is not determined by a set duration of time, but is determined in relation to the other males in his social group at the time of estrus.

Data Analysis

All "decided" agonistic interactions (Hausfater, 1975; Pereira and Kappeler, 1997) between males were used to determine male dominance ranks for each group. Agonistic outcomes for each male dyad were tallied in a matrix, as described in Bramblett (1994). This method allows for a net dominance score to be calculated for each individual and a corresponding rank to be assigned to each based upon their relative dominance score. Because more than one season of data were collected for some males, male dominance ranks as well as female sexual preference values were averaged to come up with a mean male dominance rank and a mean female sexual preference measure per male for the purposes of statistical analyses.

Two groups in two study years were identified as not having a discernable hierarchy: Group 1 in 2000, and Group 4 in 2004. Both were groups in which three of the four adult non-natal males present in the group were recent immigrants. In 2000, WCS personnel released 3 novel unrelated males into Group 1 just prior to the start of the

breeding season in September. Male dominance relationships were too variable in the short period of time prior to mating to identify a hierarchy. In the spring of 2004, three males immigrated of their own accord into Group 4. Too few agonistic interactions between the immigrants and the resident male of the group (DA, Table 2.2) were recorded to determine a male dominance hierarchy. Hence, data on female mate choice were analyzed in these groups, but analyses involving male dominance status (i.e., testing Hypothesis 1) were not performed with these two particular groups using data from these two seasons.

To quantify female multiple mating, an *index of selectivity* for each female was calculated. This selectivity index (SI) was calculated as the number of males with which a female was observed to mate divided by the total number of potential male mates ('potential mates' being sexually mature non-natal males in the vicinity at the time of her estrus). This index represents the proportion of group males mated, and provides a measure of the extent of multiple mating for each female.

Analyses were performed using non-parametric inferential statistics, including the Binomial test, Kruskal-Wallis one-way ANOVA, Mann-Whitney *U*, and Spearman rank correlation. All tests were two-tailed, and the significance level was set at 0.05. All means are reported with the standard error of the mean (SEM). Statistical tests were performed using Statistica, version 5.5.

RESULTS

Do Females Prefer Males of High Dominance Status as Mates?

Figure 5.1 shows the proportion of females per group, per mating season, who exhibited mate choice for males of different dominance rank categories. The proportion of group females showing mate choice for individual males ranged between 17-100% (Table 5.1; Figure 5.1). Despite this variability, females overall did not show more sexual preference for males of any particular dominance rank category (Kruskal-Wallis one-way ANOVA: $\chi^2 = 0.77$, df = 3, p = 0.86, NS). Lower minimum values for female sexual preference were, however, seen among males of gamma and delta rank as compared to alpha and beta males (Figure 5.1), indicating that some proportion of these lower-ranking males experience little to no female sexual proceptivity or receptivity (less than 30% of group females showed sexual preference to some of these low-ranked males).

Though females may not have solely preferred high-ranking males as mates, whether females presented first to alpha males was of interest. Indeed, in eight of thirteen instances in which the start of estrus was witnessed, alpha males were the first recipients of females' sexual presentations, which was much more frequently than would be predicted based upon the representation of these males in each social group (Binomial test: p = 0.007).

Among Non-Natal Males, Do Females Prefer Older Males as Mates?

No correlation was found between mean male age and the mean proportion of estrus females showing proceptive and receptive behaviors (Spearman rank correlation: r_S = -0.25, n = 16, p = 0.36, NS; Figure 5.2). However, there was a significant negative correlation between mean male age and the mean number of females showing proceptive or receptive behavior (Spearman rank correlation: r_S = -0.57, n = 16, p = 0.021; Figure 5.3). One male (FZ, Table 5.2) was excluded from these analyses because he became injured as a result of male-male combat and was permanently removed from the social group at the beginning of the mating season.

The negative relationship between male age and the proportion of females showing mate choice was not due to male dominance rank effects, because male dominance rank did not correlate with male age, whether each male's age was directly compared with his dominance rank per season (Spearman rank correlation: r_S = -0.17, n = 27, p = 0.38, NS), or whether a male's mean dominance rank was compared with his mean age so that each male contributed only a single data point (Spearman rank correlation: r_S = -0.1, n = 14, p = 0.73, NS).

Do Females Prefer Novel Males With Shorter Group Tenure as Mates?

No correlation was found between mean male group tenure length and the mean number of females (Spearman rank correlation: r_S = -0.358, n = 16, p = 0.173, NS) or the proportion of females who showed proceptivity or receptivity to these males (Spearman rank correlation: r_S = -0.178, n = 16, p = 0.51, NS). However, analyzing only those

groups which had both immigrants and non-natal resident males present in the same season (Table 5.1), novel males were shown sexual preference by a significantly greater proportion of estrus females than were resident males (Mann-Whitney: $n_1 = 9$, $n_2 = 10$, $U = 20.0$, $p = 0.043$; Figure 5.4).

Female Multiple Mating

To quantify female multiple mating, indices of female selectivity (SI) were calculated using data on female mating behavior in Table 5.2. Across all estrus periods witnessed (n = 40), the mean SI was 0.62±0.05 (range = SI: 0.25-1.0; number of mates: 1-4 males), indicating that females mated with over 60% of available non-natal males present in their social groups on average. For those females for whom the entire estrus period was witnessed (n = 6), the mean female SI was even higher, at 0.9±0.06 (range = SI: 0.67-1.0; number of mates: 2-4). However, because these values include some females for whom data were collected across more than one mating season, SI values were recalculated so that each female contributed only one data point. The resulting mean selectivity index across all females (n = 28) was still quite high at 0.61±0.05 (range = SI: 0.25-1.0).

To test whether the number of male mates (or female SIs) were positively related to whether a female gave birth to offspring the following year, both female SI and the number of male mates were compared with female reproductive outcome the following spring (Table 5.2). Neither the number of males mated (Mann-Whitney: $n_1 = 11$, $n_2 = 29$,

U = 127, p = 0. 338, NS) nor female SI (Mann-Whitney: $n_1 = 11$, $n_2 = 29$, U = 134, p = 0.437, NS) predicted whether the female gave birth to viable offspring the following year.

DISCUSSION

Do Females Prefer Males of High Dominance Status as Mates?

In groups where clear male dominance rankings were evident at the start of the breeding season, there was no significant difference in the proportion of group females who showed proceptive or receptive behavior to males of different dominance ranks. Indeed, there was a large amount of variability in the proportion of females showing sexual preference to males of different dominance rank categories. Differences in the proportion of females showing sexual preference were actually greater within each male dominance rank category than between different dominance rank categories. In short, females presented to and mated with both high- and low-ranking males.

However, females observed at the start of estrus were much more likely to present first to alpha males in their groups, similar to the pattern observed by Sauther (1991) among wild *L. catta* in Beza Mahafaly, Madagascar. In addition, some lower-ranked (gamma and delta) males tended to experience especially low proportions of female sexual preference on St. Catherines, with less than 30% of group females directing mate choice behaviors towards these low-ranking males, whereas no alpha or beta male experienced such a low level of female sexual interest (Figure 5.1). Females may therefore be more strongly attracted to high-ranking males, but lower-ranked males were frequently acceptable as mates.

Despite the fact that lower-ranking males also mate, the pattern of females being more likely to present first to alphas may still indicate mate choice for dominant males' "good genes" (Andersson, 1994). Many female primates often show sexual preference to the most dominant males (capuchin monkeys, *Cebus apella*: Janson, 1984; Welker et al., 1990; Phillips et al., 1994; Linn et al., 1995; Lynch, 2001; baboons, *Papio* spp.: Seyfarth, 1978; sifaka, *Propithecus verreauxi*: Brockman, 1999), especially at times of peak estrus and fertility (howler monkey, *Alouatta palliata*: Jones, 1985; golden lion tamarin, *Leontopithecus rosalia*: Baker et al., 1993; chimpanzee, *Pan troglodytes*: Matsumoto-Oda, 1999). Although endocrinological and cytological studies have confirmed that *L. catta* females are only sexually receptive during their periovulatory phase (Evans and Goy, 1968; Van Horn and Resko, 1977), the optimal time of insemination during the female's sexually receptive period is unknown. However, first-mating males may have a fertilization advantage (Pereira and Weiss, 1991), and female proceptive behavior directed preferentially to high-ranking males at the start of estrus may be interpreted as female mate choice for these dominant males. In conclusion, due to widespread female multiple mating, there was weak support for Hypothesis 1, which suggested that high-ranking males would be sexually preferred.

Do Females Prefer Older Males as Mates?

The second hypothesis tested in this study was that females would sexually prefer older males over younger males, as age might be an honest indicator of male quality (Manning, 1985). No support was found for this hypothesis. In fact, there was a negative

correlation between mean male age and the mean number of females showing sexual preference to a male, indicating that younger males mated with a significantly greater number of females on average than did older males. One explanation for this trend is that females sexually prefer younger males, a possibility which would be best tested with further data collection where male-male competition is absent, such as in a captive setting in which females have the ability to evaluate potential males in the absence of male mating competition.

An alternate possibility explaining the pattern of younger males mating with more females is that younger males on St. Catherines may have a greater ability to maintain stamina for a longer period of time during the intense male-male competition that occurs during mating periods in this species, which can involve protracted chases, lunges, and jump-fights (Jolly, 1966; Taylor, 1986; Koyama, 1988; Pereira and Weiss, 1991; Sauther 1991; Gould, 1994; Gould et al., 2005; Parga, 2006). Mean rates of aggression during *L. catta* estrus periods can sometimes exceed 35 instances of male-male aggression per hour (Parga, 2006). In addition, Sauther (1991) has noted that males visibly lose weight and have dull coats following the mating season, suggesting that male-male competition is energetically costly for *L. catta* males.

Traits involved in speed and agility may be critically important in determining male reproductive success in lemurs (Kappeler, 1990b, 1993b). Evidence in support of this idea has been found for Verreaux's sifaka (*Propithecus verreauxi verreauxi*), where reproductively successful males were found to have relatively long and muscular legs, a trait thought to be important for locomotor behaviors such as leaping (Lawler et al.,

2005). If younger males have a physical advantage over older males, this advantage may translate into higher mating success. Indeed, in a study of wild rufous lemurs (*Eulemur fulvus rufus*), Overdorff (1998) found that younger non-natal males copulated more frequently than did older non-natal males at the beginning of a female's cycle. Overdorff et al. (1999) hypothesize that these younger males may have been able to maintain an advantage over older males by being in better physical condition. Hence, among *L. catta* on St. Catherines, younger males may have greater physical stamina to remain involved in intra-sexual mating competition, which may result in these younger males mating with greater number of females than older males.

Do Females Prefer Novel Males as Mates?

The third hypothesis tested in this study was that females would prefer novel males as mates over more familiar males. Data collected in this study supported this hypothesis. Novel males received proceptive and receptive behavior from a significantly greater proportion of group females than did resident males. This evidence for female sexual preference for novel males is strengthened by findings from Chapter 4, which show that males transferring from one non-natal group to another tend to experience higher mating success (in terms of numbers of estrus females mated) in groups into which they migrate as compared to their mating success in a previous group.

These observations are in accordance with Taylor (1986), who speculated that *L. catta* females likely prefer to mate with novel males (if novel males are present), followed by resident high-ranking males. Pereira and Weiss (1991) also found strong

sexual preference for novel males in captive *L. catta* females. Matings with extra-group (novel) males have additionally been documented among *L. catta* in the wild (Sauther, 1991; Sussman, 1992; Gould, 1994). Female sexual preference for unfamiliar males has been documented in several other primate species (i.e., Japanese macaques, *Macaca fuscata*: Huffman, 1991; Takahata et al, 1999; rhesus macaques, *Macaca mulatta*: Bercovitch, 1997; olive baboons, *Papio cynocephalus*: Packer, 1979a). This sexual preference for less familiar males may be a mechanism of inbreeding avoidance (Pusey and Wolf, 1996), which likely acts in concert with female avoidance of mating with matrilineally-related males in *L. catta* (Taylor and Sussman, 1985; Taylor, 1986; Sauther, 1991; Parga, 2002a).

Female Multiple Mating in *L. catta* and Other Primates

Female multiple mating was widespread in this study. For those females who were observed throughout their entire estrus periods, each mated with at least two males, with a maximum observed number of four mates. For those females whose estrus periods were not observed in their entirety because their estrus either began at night or continued past nightfall, the numbers of mates may have been greater than was observed because night observations were not conducted. Also, because the number of males per group was small (with a maximum of four non-natal males per group), the limited number of available male mates may have set an upper boundary on the extent of female multiple mating. One possibility is that females would have mated with an even greater number of males if there were greater numbers of unrelated males per group. Indeed, the high

selectivity indices calculated for females in this study suggests that females were not being so selective as to only mate with a single male per group.

This trend of multiple mating may be considered by some as running counter to traditional sexual selection theory, which suggests that females should be highly discriminating with respect to mates (Williams, 1966; Trivers, 1972). Nevertheless, multiple-mating by females is the norm among many primate species (Hrdy, 1981; Hrdy and Whitten, 1987; Small, 1989; Dixson, 1998). Female multiple mating during periods of probable conception has been found in several anthropoids (e.g., woolly spider monkeys or muriquis, *Brachyteles arachnoides*: Milton, 1985; Strier, 1997; capuchins, *Cebus apella*: Carosi et al., 2005; blue monkeys, *Cercopithecus mitis*: Pazol, 2003; Barbary macaques, *Macaca sylvanus*: Taub, 1980; Small, 1990; Japanese macaques, *M. fuscata*: Soltis et al., 2001; rhesus macaques, *M. mulatta*: Wilson et al., 1982; chimpanzees, *Pan troglodytes*: Goodall, 1971; Stumpf and Boesch, 2005).

Female multiple mating is also seen among prosimians, both group-living and more solitary species. For example, in redfronted lemurs (*Eulemur fulvus rufus*), researchers have noted that females mate with essentially every male in their social group (Overdorff, 1998; Ostner and Kappeler, 1999). In many other prosimian species as well, females commonly mate with multiple males (aye-ayes, *Daubentonia madagacariensis*: Sterling, 1993; lesser galagos, *Galago moholi*: Pullen et al., 2000; *Microcebus murinus*: Eberle and Kappeler, 2004a, 2004b; sifaka, *Propithecus verreauxi*: Brockman, 1999; Brockman and Whitten, 1996). Female multiple mating appears to be the rule among primates, with very few exceptions.

Adaptive Theories for Female Multiple Mating

Searching for possible adaptive explanations for female multiple mating has been the subject of numerous studies (e.g. Jennions and Petrie, 2000; Soltis and McElreath, 2001). Most authors have concluded that female multiple mating must confer reproductive advantages, because females likely incur non-trivial costs as a result of this behavior, such as increased exposure to infectious diseases (Freeland, 1976), including sexually-transmitted diseases (Nunn et al., 2000; Thrall et al., 2000; Nunn, 2003; Nunn and Altizer, 2004). Multiple mating is likely adaptive for females, as this behavior is widely practiced despite its potential costs.

Several hypotheses have been proposed to explain female multiple mating. One non-adaptive explanation is that female multiple mating is simply a genetic correlate to positive selection on male multiple mating (Halliday and Arnold, 1987). Adaptive hypotheses include receiving parental care from a greater number of males (Stacey, 1982), increasing offspring genetic variability via multiple sires (Williams, 1975; Gladstone, 1979), stimulating sperm competition (Curtsinger, 1991), insuring fertilization (Gromko et al., 1984), avoiding genetic incompatibility (Zeh and Zeh, 1996, 1997), avoiding infanticide (Hrdy, 1977; 1979), and receipt of food benefits (Thornhill, 1976).

With respect to the evolution of female *L. catta* multiple mating, many of the above hypotheses are tenable, with a few exceptions. The 'food receipt' hypothesis probably cannot explain female multiple mating in *L. catta*, for females do not receive food benefits from males during courtship or copulation (Jolly, 1966; Sauther, 1991) as commonly occurs in some invertebrates (Thornhill, 1976). The "parental care"

hypothesis probably also does not explain female multiple mating in *L. catta*. Although adult males act affiliatively towards infants (grooming and playing with them occasionally), adult males do not typically provide extensive infant care (Gould, 1992, 1994, 1997; but see Gould, 2000), making it unlikely that *L. catta* females attempt to increase male alloparental care by mating with multiple males. Hence, those hypotheses positing female receipt of tangible benefits including food and parental care are less likely to explain female multiple mating in this species.

Hypotheses suggesting that females gain genetic benefits by multiple mating seem to be more plausible, including the offspring 'genetic variability' hypothesis, which suggests that females attempt to maximize the genetic variability of their offspring by increasing the number of potential sires in a single mating period (Zeh and Zeh, 1996, 1997). This hypothesis only applies where females have multiple-offspring litters or clutches (Loman et al., 1988). Therefore, whether this hypothesis could apply in *L. catta* is questionable, as multiple offspring litters are uncommon (Sauther, 1991; Jolly et al., 2002; Gould et al., 2003; Koyama et al., 2001), except for in provisioned populations such as St. Catherines Island (Parga and Lessnau, 2005) and the Duke University Primate Center, where twins and triplets have been documented (Pereira, 1993b). The genetic variability hypothesis requires that multi-male parentage be possible, but whether more than one male can sire different offspring in *L. catta* twin or triplet births is currently unknown.

A more likely functional explanation is that multiple mating in *L. catta* serves to stimulate sperm competition (Parker, 1970), which would allow the male with the most

able sperm to attain fertilization success, selecting for higher quality sperm (and female multiple mating) over successive generations (Yasui, 1997, 1998). Another theory is that female multiple mating may allow females to avoid genetic incompatibility between herself and potential sires (Zeh and Zeh, 1996, 1997), though genetic data are needed to definitively evaluate this hypothesis.

Two adaptive hypotheses in particular have been suggested to explain female multiple mating in many non-human primates: the infanticide avoidance hypothesis, and the fertilization assurance hypothesis. These two hypotheses are discussed in detail below to determine their suitability as explanations for female multiple mating in *L. catta*.

Female Multiple Mating as Infanticide Avoidance?

Infanticide as an adaptive reproductive strategy of male primates has long been an issue surrounded by intense debate (Bartlett et al., 1993; Sussman et al., 1995; Hrdy et al., 1995; Sommer, 2000). Proponents of sexually selected male infanticide suggest that males kill the offspring of other males in order to increase their own chances of reproducing with the offspring's mother (Hausfater and Hrdy, 1984). Females are expected to have evolved various counter-strategies to male infanticide, such as association with males who are effective protectors of infants (van Schaik, 1996), or the promiscuous strategy of mating with multiple males to confuse paternity (Hrdy, 1977, 1979; 2000; van Schaik et al., 1999, 2000). Sexually selected male infanticide has been implicated in many mammals, including carnivores, rodents, and several anthropoid primates (Hausfater and Hrdy, 1984; Pusey and Packer, 1994; van Schaik and Janson,

2000). In some primates, there is compelling genetic evidence showing that males kill infants that are not their own, and go on to mate with the killed infant's mother, likely siring future offspring (Hanuman langurs, *Presbytis entellus*: Borries et al., 1999). Reports of infanticidal behavior by males in some prosimian species have also been interpreted as fitting with the sexual selection model for infanticide (e.g., Milne-Edward's sifaka, *Propithecus diadema adwardsi*: Wright, 1995; Erhart and Overdorff, 1998).

However, whether infanticide is a sexually selected strategy for *L. catta* males is a contentious topic, with agreement (Pereira and Weiss, 1991; Pereira et al., 1999) and disagreement (Sauther and Sussman, 1993; Sauther et al., 1999; Sussman, 1999) strictly demarcated on both sides. Male attacks on infants have been observed at one site in the wild, Berenty (Hood, 1994; Jolly et al., 2000; Ichino, 2005), and at one captive location, the Duke University Primate Center (Pereira and Weiss, 1991; Jolly et al., 2000).

Nevertheless, the validity of male infant-killing behavior as an adaptive strategy has been questioned for several reasons (see Sauther et al., 1999 and Sussman, 1999), including a conspicuous lack of male infanticidal behavior at sites where *L. catta* have been well-studied for many years (e.g., Beza Mahafaly: Sauther, 1991; Sauther and Sussman, 1993; Gould, 1994). Because *L. catta* females in the wild commonly mate with both troop and extra-troop males during estrus (Jolly, 1966; Koyama, 1988; Sauther, 1991; Sussman, 1992; Gould, 1994), males would need to be able to identify their own offspring and only target the offspring of other males for infanticide to be adaptive in this species. Furthermore, because *L. catta* breed seasonally (Jolly, 1984; Rasmussen, 1985), females also would not come into estrus any sooner as a result of infant loss via

infanticide. Concerning this last point, Pereira and Weiss (1991) suggest that losing an infant in one year should increase the chances of survival for the infant born to the female in the following year, though this suggested trend of increased infant survival following infant loss in the previous year has not been demonstrated for any *L. catta* population to date.

Infanticide by males was not observed during the course of the present study, and has not been witnessed on St. Catherines Island (Parga and Lessnau, 2005; Lessnau, pers. comm.). Therefore, infanticide does not appear to be a mating strategy employed by male *L. catta* on St. Catherines. Consequently, female multiple mating at this site does not appear to function in infanticide avoidance. Instead, a more likely possibility is that multiple mating by females has been selected for due to its functionality in ensuring fertilization.

Female Multiple Mating as Fertilization Assurance?

Just as males are expected to increase their reproductive success by attempting to maximize the number of females with which they mate (Bateman, 1948), females should also attempt to maximize their reproductive gain by mating with multiple males to ensure conception (Small, 1988). In the present study, the number of mates per female did not show a significant positive relationship with whether a female conceived the following year, which seems to suggest that fertilization assurance is not an adequate explanation for female multiple mating in this species. However, the numbers of observed mates for many of the females in this study were likely underestimated because so few females

were observed across their entire estrus cycle. To definitively test the fertilization assurance hypothesis for female multiple mating, a much larger sample size of females is needed for whom the entire estrus period is witnessed to compare fertilization rates with numbers of mates to test if there is a positive correlation between the two variables.

Given that *L. catta* females breed seasonally (Rasmussen, 1985), and under normal conditions will only give birth to one offspring per year (Sauther, 1991; Pereira, 1993b; Koyama et al., 2001; Jolly et al., 2002; Gould et al., 2003; Parga and Lessnau, 2005), a female who does not reproduce during one year will likely do so at a cost to her lifetime reproductive success, potentially producing strong positive selection for females who mate with more than one male during estrus. In conclusion, female multiple mating may be an adaptive female strategy to ensure fertilization in this species, as previously suggested by Koyama (1988) and Sauther (1991).

Inter-Sexual Conflict

Inter-sexual conflict occurs when the evolutionary interests of males and females come into opposition, such as when a mating advantage to a male causes a disadvantage or cost to his female mate (Parker, 1979). Inter-sexual conflict can result in various ways in primate mating systems. One salient example seen of inter-sexual conflict in primates is when male mate guarding behavior coexists with female mate choice for males other than the guarding male. Female primates can circumvent and combat male mate guarding efforts using many behavioral strategies. For example, females can make male mate guarding more difficult via avoidance of the guarding male, or by actually hiding

from guarding males (capuchins, *Cebus apella*: Lynch, 2001; olive baboons, *Papio cynocephalus*: Smuts, 1985; Strum, 1987), actively approaching competitor males, and/or participating in copulations with non-dominant or non-group males (e.g., gibbons, *Hylobates* spp.: Palombit, 1994; Reichard, 1995; chimpanzees, *Pan troglodytes*: Gagneux et al., 1997). Where the male strategy used is sexual coercion (Smuts and Smuts, 1993) in the form of forced copulation or sexual harassment, females can circumvent such aggressive male mating strategies in several ways. One strategy used by orangutan (*Pongo pygmaeus*) females is to keep close proximity to adult males, and in so doing, decrease the likelihood of experiencing sexual harassment from subadult males (Fox, 2002).

Male and female mating strategies can easily come into direct conflict given that female multiple mating appears to be a female mating strategy in *L. catta*. Despite the fact that females are dominant in this species (Jolly, 1966), female *L. catta* cannot easily circumvent the activities of a guarding male because female aggression toward the guarding male is not always effective in stopping males from guarding (Parga, personal obs.; Sauther, pers. comm.). Though not all males mate guard, many *L. catta* males are able to mate guard for a limited amount of time (Chapter 2), thereby keeping females from gaining proximity to other males for that time period. Female *L. catta* can circumvent the guarding strategies of males by participating in sneak copulations (Chapter 2), or by approaching and soliciting competitor males following the completion (mating to ejaculation) of a previous male's mating bout (Parga, unpub. data). In this

way, *L. catta* males and females appear to circumvent one another's reproductive strategies, and show inter-sexual conflict.

CONCLUSIONS

Only weak support was found for Hypothesis 1, which predicted that high-ranking males would be sexually preferred over low-ranking males. There was no statistically significant difference in the proportion of estrus females per group which showed receptivity or proceptivity to males of different dominance rank categories. However, in cases where females were observed at the start of estrus, the first male presented to was significantly more likely to be an alpha male, which may suggest that females are more strongly attracted to alpha males.

No support was found for Hypothesis 2, which predicted that older rather than younger males would be preferred as mates. Instead, an analysis of female proceptivity and receptivity by male age showed that younger males mated with a significantly greater number of estrus females than older males. This trend may indicate that females sexually prefer these younger males, or that younger males on St. Catherines have superior stamina compared to older males. Further research is needed to discern between possibilities, perhaps testing female sexual preferences for males of different ages in captivity under conditions where male-male competition is absent.

Hypothesis 3 predicted that more novel males (those who had been in groups for a shorter period of time than other male group residents) would be shown greater female sexual preference than more familiar group males. Data supported this hypothesis.

Novel males received proceptive and receptive behavior from a significantly greater proportion of group females than did resident males. Female sexual preference for novel males could be a mechanism of inbreeding avoidance.

Female multiple mating was extremely widespread in this study. In several cases females mated with most or all of the males in their social groups, resulting in high female selectivity index values. Admittedly, the numbers of males per group were few, numbering between two and four non-natal males. However, the fact that all females who were observed throughout estrus mated with at least two males indicates strongly that females are not limiting their sexual preference to solely a single male per group. Of the several possible adaptive explanations for female multiple mating, the infanticide avoidance hypothesis was deemed an unlikely explanation for the *L. catta* on St. Catherines Island; instead, female multiple mating may function as fertilization assurance. The fertility assurance hypothesis needs to be retested in *L. catta* with a large sample size of females that are observed throughout their estrus periods so that the total number of mates can be recorded per female. In conclusion, patterns of mating in *L. catta* indicate inter-sexual conflict, as the pervasive female mating strategy appears to be to mate with more than one male, while males attempt to sequester them from other males via aggressive male-male competition.

Table 5.1: List of all non-natal males, their dominance ranks, ages, residency status, and females who showed mate choice for them

Study year	Group	Male	Male dominance rank	Male age (yrs.)	Resident or novel?[1]	Group tenure length (yrs.)	Females who showed proceptivity or receptivity	# of females showing preference to this male	Proportion of estrus females showing preference
2000	3	BY	1	5	Resident	3.25	AN,MA,UR	3	0.5
2000	3	ED	2	9	Resident	3.17	AN,JN,LS,MA	4	0.67
2000	3	MC	3	13	Resident	6.67	RR	1	0.17
2000	1	EK	N/A	2	Resident	0.5	LB	1	0.25
2000	1	FD	N/A	10	Novel	0.08	JL	1	0.25
2000	1	RK	N/A	3	Novel	0.08	HP,JL,LB	3	0.75
2000	1	SP	N/A	4	Novel	0.08	BT,HP,JL	3	0.75
2001	3	BY	1	6	Resident	4.25	AN,JN,MA,RR	4	0.8
2001	3	KL	2	8	Novel	0.58	AN,JA,JN,MA, RR	5	1
2001	3	MN	3	2	Novel	0.58	AN,JA,MA,RR	4	0.8
2001	3	MC	4	14	Resident	7.67	RR	1	0.2
2001	1	SP	1	5	Resident	1.08	JL,KY	2	1
2001	1	EK	2	3	Resident	1.5	JL,KY	2	1
2001	1	FD	3	11	Resident	1.08	JL,KY	2	1
2002	2	ED	1	11	Resident	1.83	JO,SHL,TO	3	0.6
2002	2	BR	2	4	Resident	1.58	JO,SHL,TO	3	0.6
2002	2	RY	3	3	Resident	1.42	JO,QU,SHL,TO, VT	5	1
2002	2	CH	4	3	Resident	1.42	JO,QU,SHL,TO, VT	5	1
2002	3	KL	1	9	Resident	1.67	CA,MA	2	1
2002	3	MN	2	3	Resident	1.67	CA,MA	2	1
2002	3	BY	3	7	Resident	5.33	CA,MA	2	1

Table 5.1 (continued): List of all non-natal males, their dominance ranks, ages, residency status, and females who showed mate choice for them

2003	2	BR	1	5	Resident	2.58	TO	1	0.33
2003	2	ED	2	12	Resident	2.83	TO	1	0.33
2003	2	RY	3	4	Resident	2.47	KA,TO	2	0.67
2003	2	LE	4	3	Novel	0.58	KA,MY,TO	3	1
2003	3	CP	1	2	Novel	0.003	DB,JK,JN,MA, RA,RR	6	0.75
2003	3	MX[2]	3	1	Novel	0.003	AN,JN,MA,RA	4	0.5
2003	3	KL	2	10	Resident	2.58	AN,JK,JN,MA, RR	5	0.63
2003	3	MN	3	4	Resident	2.58	AN,JA,JK,JN, MA,RR	6	0.75
2004	3	KL	1	11	Resident	3.58	HO	1	0.5
2004	3	MN	2	5	Resident	3.58	HO,JN	2	1
2004	4	BR	N/A	6	Novel	0.75	KT,ND,RO	3	0.75
2004	4	DA	N/A	4	Resident	2.75	KT,SU	2	0.5
2004	4	ED	N/A	13	Novel	0.75	KT,ND,RO	3	0.75
2004	4	FZ[3]	N/A	2	Novel	0.75	ND	1	0.25

[1]Residency status for each male is determined by the tenure status of other males in the group. Seasonal immigrants are considered novel when compared to resident males that have been in the group for a year or more. However, seasonal immigrants are considered resident if they have been in the group for several months, and other more novel males have transferred into the group within a month's time or less.

[2]An average dominance rank had to be calculated across the mating season for this male, as his rank altered due to a change in group composition. Resident males KL and MN were locked in the group's shelter site due to injury for the first part of the breeding period, at which time he was ranked second. Upon their release, this male was ranked fourth when dominance relationships were reestablished.

[3]This male's values for female sexual preference are incomplete; he was removed from the group permanently at the beginning of the mating season due to a serious wound incurred from male-male competition.

Table 5.2: Females observed to mate in each season, their selectivity indices, and numbers of mates

Study year	Group	Female	Was entire estrus period witnessed?	Selectivity index	Number of observed mates (males who mounted)	Offspring the following year as a result of this mating?
2000	1	BT	No	0.25	1	No
2000	3	UR	No	0.33	1	Yes
2000	1	LB	No	0.5	2	Yes
2000	3	LS	No	0.33	1	Yes
2000	3	MA	Yes	0.67	2	Yes
2000	1	HP	No	0.25	1	Yes
2000	3	JN	No	0.33	1	Yes
2000	1	JL	No	0.5	2	Yes
2000	3	AN	No	0.33	1	Yes
2001	3	JA	No	0.5	2	Yes
2001	3	MA	Yes	0.75	3	Yes
2001	3	RR	Yes	1	4	Yes
2001	3	JN	No	0.25	1	Yes
2001	1	KY	No	1	3	Yes
2001	1	JL	No	1	3	Yes
2002	2	SHL	No	1	4	Yes
2002	2	JO	No	1	4	No
2002	2	QU	No	0.5	2	No
2002	2	VT	No	0.5	2	Yes
2002	2	TO	No	1	4	No
2002	3	MA	Yes	1	3	Yes
2002	3	CA	No	1	3	No
2003	2	MY	No	0.25	1	No
2003	2	TO	No	1	4	Yes
2003	2	KA	No	0.5	2	Yes
2003	3	JN	Yes	1	2	Yes
2003	3	MA	No	0.5	1	No
2003	3	RR	No	0.5	1	No
2003	3	AN	No	0.5	1	No
2003	3	RA	No	1	2	Yes
2003	3	JK	No	0.67	2	Yes
2003	3	DB	No	0.33	1	No
2003	3	JA	No	0.25	1	Yes
2003	3	MA	No	0.75	3	Yes
2004	3	JN	No	0.5	1	Yes
2004	4	ND	No	0.75	3	Yes
2004	4	KT	Yes	1	3	Yes
2004	4	RO	No	0.33	1	Yes
2004	4	SU	No	0.33	1	No
2004	3	HO	No	0.5	1	Yes

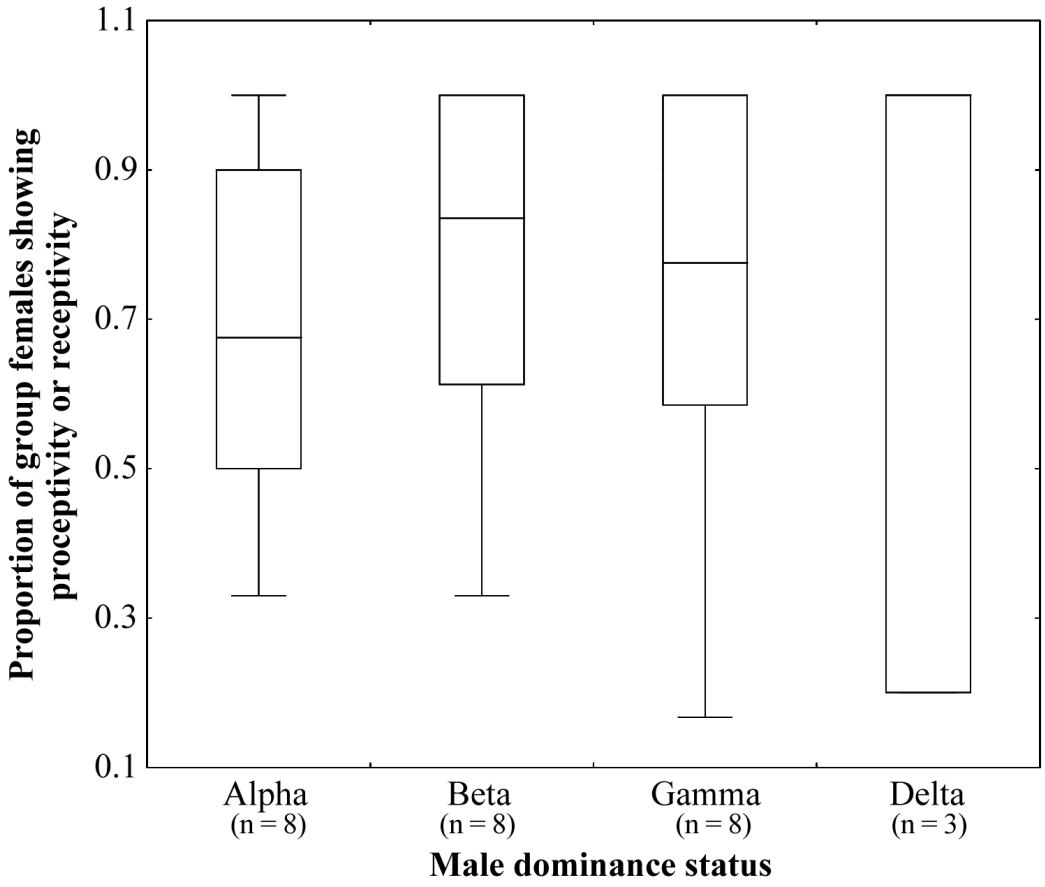

Figure 5.1: Proportion of group females showing proceptivity or receptivity to males of different dominance ranks. There was no significant difference in the proportion of group females that showed proceptivity or receptivity towards males of each dominance rank (Kruskal Wallis: $\chi^2 = 0.77$, df = 3, p = 0.86, NS). Boxes represent the interquartile range, whiskers represent maximum and minimum values, and lines represent median values.

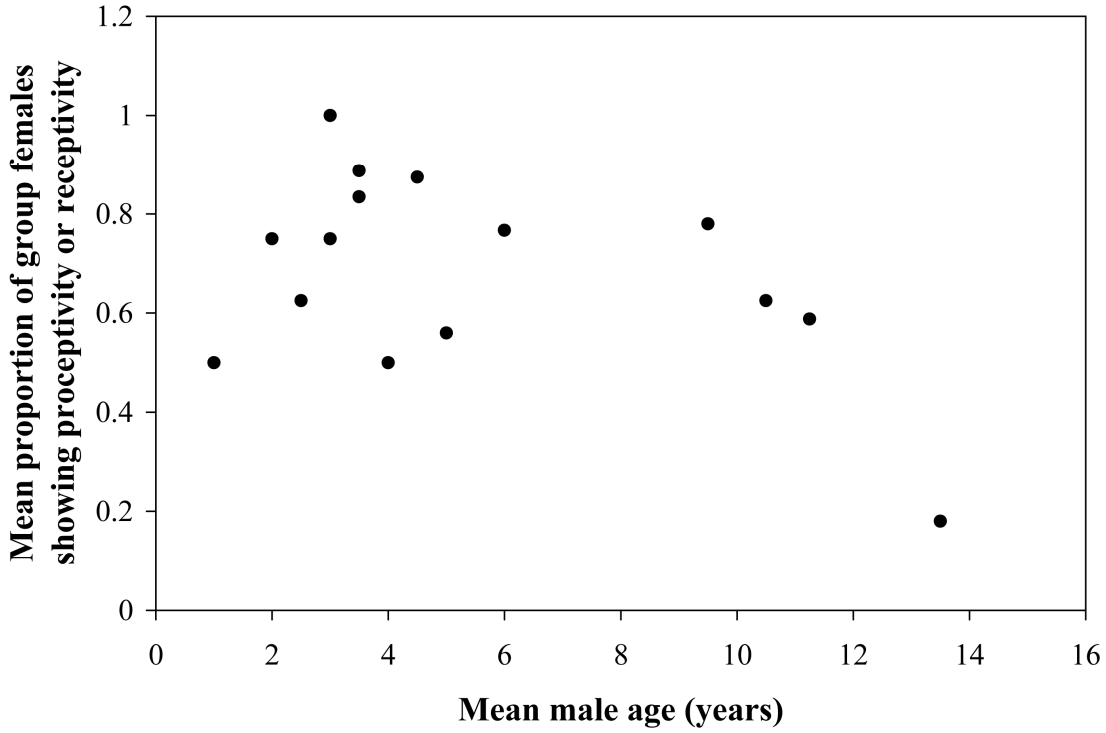

Figure 5.2: Mean proportion of group females showing proceptivity or receptivity by mean male age. Mean male age and mean proportion of group females showing proceptive and receptive behaviors did not significantly correlate (Spearman rank correlation: $r_S = -0.25$, n = 16, p = 0.36, NS).

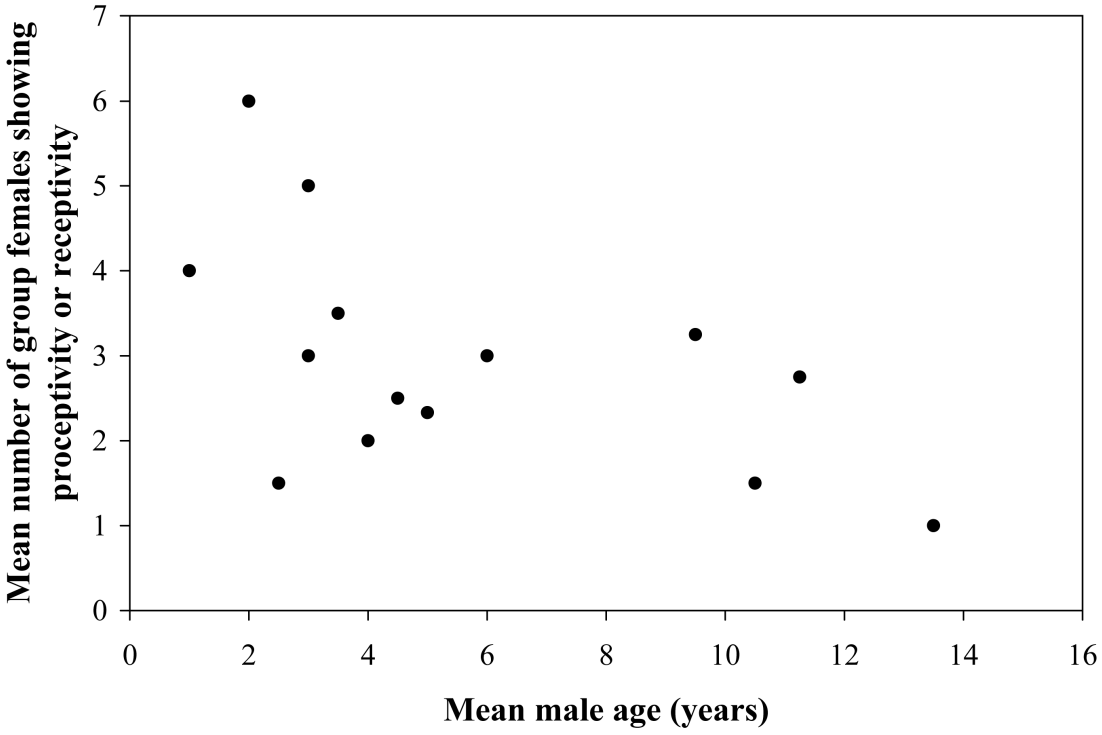

Figure 5.3: Mean number of group females showing proceptivity or receptivity by mean male age. Mean male age and mean number of group females showing proceptive or receptive behavior were significantly negatively correlated, suggesting that more females exhibited sexual preference towards younger males (Spearman rank correlation: $r_S = -0.57$, $n = 16$, $p = 0.021$).

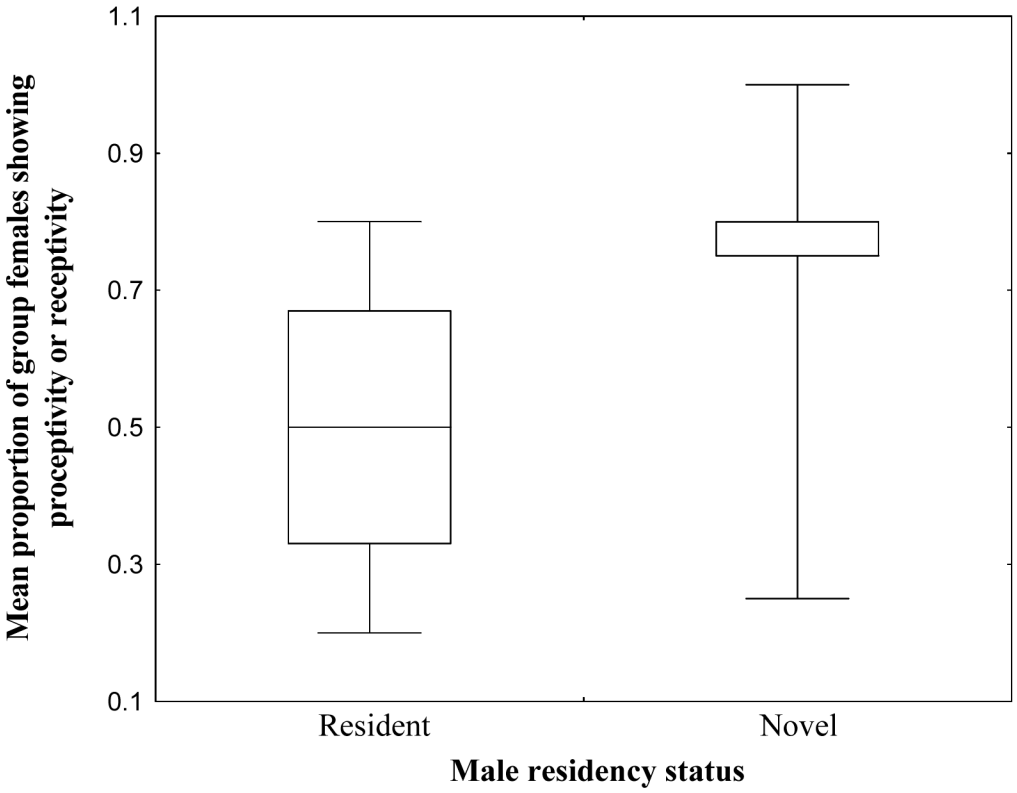

Figure 5.4: Mean proportion of group females showing proceptivity or receptivity by male residency status. There was a significant difference in the mean proportion of group females that showed proceptivity or receptivity to males of different residency status, with females showing stronger sexual preference for novel males (Mann-Whitney: $n_1 = 9$, $n_2 = 10$, $U = 20.0$, $p = 0.043$). Boxes represent interquartile range, whiskers represent maximum and minimum values, and lines represent median values.

CHAPTER 6: A CASE STUDY:

THE SEXUAL COERCION OF A *LEMUR CATTA* FEMALE

INTRODUCTION

Sexual Coercion is Not Expected Where Female Dominance Prevails

Sexual coercion by males towards females occurs when, in a reproductive context, males increase their likelihood of paternity as a result of force (or the threat of it) at a cost to the female (Smuts and Smuts, 1993). Instances of forced copulation (e.g. oranguatans, *Pongo pygmaeus*: MacKinnon, 1974; Mitani, 1985), male aggression towards females which functions as harassment or intimidation (e.g. chimpanzees, *Pan troglodytes*: Goodall, 1986; Japanese macaques, *Macaca fuscata*: Soltis et al., 1997), and sexually selected male infanticide (Hrdy, 1979; Van Schaik, 2000) have all been identified as forms of male sexual coercion (Clutton-Brock and Parker, 1995). Though often found among primates where males habitually dominate females, male sexual coercion would not generally be expected in a primate in which females agonistically dominate males. Nevertheless, during the present study, an instance of male sexual coercion in a female dominant primate (Richard, 1987) was documented.

Female social dominance is a trait shown by some, but not all of the Malagasy lemurs (Pereira et al., 1990). *L. catta* is considered an unequivocally female dominant species, for adult females are able to consistently elicit submissive behavior from males in both feeding and non-feeding contexts (Jolly, 1966, 1984; Budnitz and Dainis, 1975; Taylor and Sussman, 1985; Taylor, 1986; Kappeler, 1990a, 1993a; Pereira et al., 1990;

Sauther, 1992; Gould, 1994; Nakamichi and Koyama, 1997; Pereira and Kappeler, 1997; Sauther et al., 1999). However, there is an ontogenetic progression to the development of female social dominance in *L. catta* (Gould, 1990; Pereira, 1993c, 1995; Sauther et al., 1999). Female *L. catta* typically do not attain dominance over males until after their first mating season, which occurs at two years of age in the wild (Sauther, 1993).

Background: *Lemur catta*

L. catta groups have multiple males and females in a roughly 1:1 sex ratio, and group size can range between 5-27 individuals (Jolly, 1966, 1972; Budnitz and Dainis, 1975; Sussman, 1974, 1977, 1991; Mertl-Milhollen et al., 1979; Jolly et al., 1982b, 2002; Sauther, 1992; Gould, 1994; Gould et al., 2003; Pride, 2003, 2005). This species breeds seasonally, and females only copulate during estrus, which is a short period lasting less than one day in most cases (Jolly, 1966, 1967; Evans and Goy, 1968; Van Horn and Resko, 1977; Koyama, 1988; Sauther, 1991; Koyama et al., 2001; Pereira and Weiss, 1991, Parga, 2006). Furthermore, *L. catta* experience asynchrony in estrus, so there will usually only be a single female in estrus at any given time in a social group (Pereira, 1991; Sauther, 1991). *L. catta* kept under natural light conditions mate during the fall and winter months in the Northern hemisphere (Evans and Goy, 1968; Pereira and Weiss, 1991), which is 6 months out-of-phase with these occurrences in Madagascar (Van Horn, 1975).

Female *L. catta* often mate with more than one male during estrus, and female mate choice has been documented in captive (Van Horn and Resko, 1977; Taylor and

Sussman, 1985; Taylor, 1986; Pereira and Weiss, 1991) and wild individuals (Koyama, 1988; Sauther, 1991; Gould, 1994, 1996). The copulatory pattern exhibited by this species involves several separate mounts (some with and some without intromission) before ejaculation is achieved, and males only ejaculate once with a female during a single estrus period (Sauther, 1991; Parga, 2003; Parga et al., 2006). *L. catta* can therefore be placed in category #10 (no copulatory lock, thrusting, multiple intromissions, single ejaculation) according to the schema devised by Dewsbury (1972) to describe mammalian mating patterns. Separate copulatory mounts are frequently interspersed with male-male agonism (Jolly, 1966, 1967; Koyama, 1988).

L. catta females usually do not enter estrus until two years of age in the wild and give birth for the first time at the primiparous age of three (Sussman, 1977, 1991; Koyama et al., 2001; Gould et al., 2003). However, females that are food provisioned or exist in resource-rich areas in the wild can enter estrus at one year of age and give birth to their first infant at the age of two (Berenty, Madagascar: Koyama et al., 2001; Duke University Primate Center, USA: Taylor, 1986; Pereira, 1993c; St. Catherines Island, USA: Parga and Lessnau, 2005).

This Study: Unexpected Documentation of Male Sexual Coercion

As part of the present study of male mating strategies and female mate choice in *L. catta*, an instance of male sexual coercion (Smuts and Smuts, 1993; Clutton-Brock and Parker, 1995) of a one-year-old nulliparous estrus *L. catta* female was documented. The form of sexual coercion witnessed took the form of a forceful mating attempt which was

only partially met with acquiescence by the female, who frequently attempted to extricate herself from the male's mounted grasp but was unable to physically overcome the male. The present chapter describes this event in detail, and discusses the implications of this male behavior in reference to male mating strategies, sexual selection, and the ontogeny of female social dominance.

METHODS

Study Site and Study Animals

Provisioned, free-ranging *L. catta* groups have been maintained on St. Catherines Island, Georgia, USA (Thomas et al., 1978; Thomas, 1988) by the Wildlife Conservation Society since 1985 (Keith-Lucas et al., 1999). This site (located at 31º 40' N latitude, 80º 41' W longitude) is a privately-owned, largely undeveloped semi-tropical barrier island measuring 2,900 hectares, with a mixture of habitats, including pine, oak and palmetto forests, and open pastures as well as savanna and marsh (Keith-Lucas et al., 1999).

Keith-Lucas et al. (1999) provide a brief history of the *L. catta* colony on St. Catherines Island, including a description of lemur behavior following the initial release of a founder population of six individuals. The lemurs on St. Catherines are provisioned daily with food (a mixture of monkey chow and fruits and/or vegetables), and water. The lemurs also forage on naturally-occurring vegetation, show ranging behaviors, and have established home range areas (Dierenfeld and McCann, 1999; Keith-Lucas et al., 1999). All adult lemurs have been fitted with uniquely-colored Telonics radio collars (Mesa,

AZ). Subadults and small adults were often fitted with nylon collars. Differences in physical characteristics and shaving patterns were used to identify uncollared animals.

At one time, the *L. catta* colony on St. Catherines grew to over 75 individuals in four free-ranging groups (Parga and Lessnau, 2005). Each of these groups was studied across the duration of this project, though different groups were studied in each year. Table 2.1 shows the groups that were studied during the start and middle of the breeding season in each year of this project (spanning late October-December). Table 2.2 shows the composition of each study group in early October (prior to the start of the mating season) of each year. The lemur group in which the instance of sexual coercion occurred was Group 2 during 2002, which contained 8 females one year of age and older, and 4 non-natal males one year of age or older (Table 2.2).

Data Collection on Mating and Social Behavior

A. Breeding Season

Due to photoperiodic regulation, reproduction in *L. catta* on St. Catherines Island is approximately six months out-of-phase with the timing of these events in Madagascar, the endemic habitat of *L. catta* (Rasmussen, 1985). Mating behavior is limited to the fall and winter months (September-February) in the northern hemisphere if the lemurs are exposed to natural light (Evans and Goy, 1968; Van Horn, 1975). Data on mating behavior were collected during five consecutive breeding seasons: October-December 2000-2004, with additional data collected on mating behavior late in the breeding season of one year, during January-February 2004. The instance of sexual coercion described in

this chapter was witnessed in November 2002 during the first estrus cycle of the breeding season, which typically begins during the last few days of October and the first weeks of November yearly at this location (Parga, unpub. data).

During breeding periods, data were collected daily from "dawn to dusk" using 'all-occurrences' sampling (Altmann, 1974) of agonism and reproductive behavior. In mating contexts, the following behaviors were recorded (in addition to recording the agonistic behaviors listed in section "B. Non-Breeding Season" below): jump-fights, mounts, thrusting, and female sexual presents. Female sexual presentations are conspicuous in this species, and can involve a lordosis posture by the female (Evans and Goy, 1968). If observable, penile intromission, ejaculation, and copulatory plug displacement (Parga, 2003) were also recorded, though observation conditions did not always allow these more detailed sexual behaviors to be verified. Ejaculation was indicated by the presence of semen in the female's peri-vaginal area, and/or on the tip of the male's penis. The start time (and stop time, if appropriate) of each behavior was recorded in seconds. Behavioral estrus was indicated by proceptive (sexual solicitation) or receptive (allowance of male mounting) behavior (Beach, 1976).

During the 2001 through 2004 breeding seasons, one to two field assistants helped monitor groups for estrus behavior and collect social and reproductive data. One observer was stationed per group unless a female was in estrus in one of the groups, in which case two observers paired up at the group with the estrus female.

B. Non-Breeding Season

During the pre-breeding months of each year (June-September in 2000 and 2004, and September-October 2001–2003), data on social behavior were collected approximately five days per week between the hours of 0600 and 1900, with the majority of samples collected between 0800 and 1600. Information on dominance relationships among males was gathered during this time via two main sampling techniques: continuous-time focal animal sampling, and 'all-occurrences' sampling for agonism (Altmann, 1974). Each sampling technique was performed separately, alternating between the two sampling types throughout the day. Each type of sample lasted for 20 minutes during 2000-2001, and was thereafter shortened to 15 minutes in duration. Focal sampling order was randomized, with no more than two samples per individual per day.

During focal samples, the following 'state' behaviors (Martin and Bateson, 1986) were recorded to the nearest second: rest, travel, feed, auto-groom, and allo-groom. The following 'event' behaviors (Martin and Bateson, 1986) were scored: approach, defecate, urinate, scent-mark (ano-genital, palmar, shoulder, tail), approach-withdraw, bite, chase, cuff, fight, grapple, lunge, nose-push, push, stink-fight, take food, and tail-wave (Jolly, 1966; Petter and Charles-Dominique, 1979; Taylor, 1986; Gould, 1994; Pereira and Kappeler, 1997; Parga, 2002a). *Ad libitum* data were collected at all times during all seasons of the year in both non-mating and mating periods to record sporadic or infrequent events such as predation attempts on the lemurs, instances of mobbing, and alarm or howling vocalizations.

Data Analysis

Male dominance ranks were calculated based upon all "decided" agonistic interactions (Hausfater, 1975; Pereira and Kappeler, 1997) between males. Agonistic outcomes for each male dyad were tallied in a matrix, as described in Bramblett (1994). This method allows for a net dominance score to be calculated for each individual and a corresponding rank to be assigned to each based upon their relative dominance score.

To generate a quantitative measure of female sexual preference for each male, the total number of female sexual presentations to each male was used. Although male mate guarding in this species (Sauther, 1991; Parga, 2003, Chapter 2) sometimes constrains females' ability to gain proximity to other group males, this particular female was not mate-guarded consistently by any single male, and was able to gain proximity to all group males during her period of sexual receptivity. Hence, her presentation frequency to each male was considered an appropriate measure of her sexual preference for each male.

Mating is defined here as a male mounting a female. A male's mating success was measured as the number of estrus females he was observed mating. Additionally, a "success ratio" for each male was calculated following Michael et al. (1967) and Brockman (1999) to measure the percentage of successful mounts out of the total number of mounts attempted. A "successful" mount is defined here as a mount in which the female acquiesced with copulation, neither directing aggression at the male nor withdrawing from him.

Analyses were performed using non-parametric statistics. Chi-square goodness-of-fit tests were run on several variables (female sexual presentation frequency, male success ratio, number of mounts attained, cumulative time spent in mounts) to test for a significant difference among males with respect to each measure. Expected values for each test were calculated using the mean of the observed values for each measure. Spearman rank correlation was also used to test for agreement between variables. The level of statistical significance was set at 0.05.

RESULTS

During the 2002 mating season, a yearling nulliparous female in Group 2 (TO, Table 2.2) was observed to enter estrus on November 8. She was the last of five females observed to enter estrus in the study troop, and was the only yearling observed mating in this troop. This female mated with all four resident non-natal males, but only one of the males acted sexually coercive towards her, male BR (Table 2.3). Dominance relationships among males in this group were linear, and the sexually coercive male BR was ranked second (beta) out of the group's four males during the pre-breeding period (Table 2.3).

The sexually coercive male was one of the two group males with the lowest mating success this breeding season, as measured by the number of estrus females each was observed mounting (Figure 6.1). Despite their high dominance status, male BR and the alpha male of the group, ED, were only observed to mate with three of the five troop females observed to enter estrus. The other two males (CH and RY) mated with all five

females observed in estrus that breeding season (Figure 6.1, Table 5.1). None of the other males acted sexually coercive towards any of the estrus females in this group, and male BR did not direct coercive behavior towards any female besides TO.

Description of Male Sexual Coercion of a Yearling Female

The sexual coercion of female TO began approximately 35 minutes following the female's first exhibition of estrus (her first sexual present), after she had already been mounted but not inseminated by two other males, CH and RY (Table 2.3). The sexually coercive male's first mount attempt was unsolicited by the female, and when she rebuffed his advances, the pair began to grapple. The female and sexually coercive male intensely grappled on seven different occasions throughout the multiple mounts of the copulation. If not for the fact that the estrus female actually presented to this coercive male and allowed him to mount on some occasions (in between rejections), the occurrence would have largely appeared to be an attempt by the male at forced copulation. Although some of the sexually coercive male's actual and attempted mounts were solicited by the yearling female in the form of sexual presents, 66% were unsolicited by the female (Figure 6.2). About half of his unsolicited mount attempts were rejected and met with aggression (Figure 6.2).

On several occasions during mounts that were aggressively rejected by the female, the male continued to forcefully clasp the female's midsection, and remained mounted while actively thrusting. On at least one occasion the male gained penile intromission, and proceeded to thrust while the female attempted to extricate herself

unsuccessfully from the male's grasp, directing cuffs at him. In one instance when the female was cuffing and attempting to withdraw from the male, the female's mother (JO, Table 2.2) came to her aid and cuffed the male away.

The female's intermittent acceptance and rejection of the sexually coercive male did not appear to be due to a change in her proceptivity over time, because there was no clear pattern of acceptance versus rejection of his mount attempts. Also, she solicited copulations from other males between the sexually coercive male's mounts.

The female was observed in estrus for approximately 4 hours and 40 minutes, as measured from the time of her first sexual present until the end of observations that day (at nightfall). The female was still mating when observations ceased; hence, the female's entire estrus period was not witnessed. At the time that observations were ended, no male had yet ejaculated, and all estrus behavior had ceased as of the following morning. Whether this female conceived is not conclusively known, but she was not observed to produce any offspring in the subsequent birth season.

Male Success Ratios and Female Sexual Preference

The number of presentations received by each male and his success ratio (proportion of mounts met with sexual acquiescence) were positively correlated (Spearman rank correlation: $r_S = 1.0$, $n = 4$; Figure 6.3). Of the four males with whom the female mated, the sexually coercive male was the second-to-least preferred (as measured by sexual presents), and also had the second-to-lowest success ratio of all the males (Figure 6.3). Both the number of sexual presents directed to each male (Chi-square

goodness of fit: $\chi^2 = 20.53$, df = 3, $p < 0.0001$) as well as male success ratios differed significantly from one another (Chi-square goodness of fit: $\chi^2 = 32.75$, df = 3, $p < 0.0001$). As is evident, the sexually coercive male, BR, was neither one of the most preferred males, nor one of the males with the greatest proportion of mounts accepted.

Figure 6.4 shows the ratio of sexual presentations (solicitations) by the female relative to the number of mounts achieved by each male. Values above one indicate that the number of sexual presents by the female to a particular male exceeded the actual number of mounts he achieved. Values below one indicate that the number of mounts was greater than the number of presents received. Of all the males, the sexually coercive male, BR, achieved the lowest proportion of presents to mounts (Figure 6.4).

Remarkably, though the sexually coercive male BR was neither presented to at a high frequency nor had a high mounting success ratio (Figure 6.3), he nevertheless achieved the greatest number of mounts of all males, and furthermore, showed the longest cumulative time spent in mounts (Figure 6.5). Both the number of mounts by each male (Chi-square goodness of fit: $\chi^2 = 27.24$, df = 3, $p < 0.0001$) and the cumulative time spent in mounts differed significantly among males (Chi-square goodness of fit: $\chi^2 = 323.26$, df = 3, $p < 0.0001$). There was also a significant positive correlation between the total number of a male's observed mounts and the cumulative time he spent in mounts (Spearman rank correlation: $r_S = 1.0$, n = 4; Figure 6.5).

Other Males Were Not Sexually Coercive

Other males' responses to the female's sexual rejection were non-aggressive. With the exception of BR, the coercive male, the other three males either immediately withdrew from the female upon receiving a cuff from her, often emitting a submissive yip or squeal vocalization (Jolly, 1966; Macedonia, 1993) while retreating, or they did not persist in following the female if she walked away from their mount attempt.

Two other forms of agonism (grappling) were directed at this female during her estrus. In one instance, the female grappled with a same-age natal male for approximately 18 seconds following the male's tail-wave (Jolly, 1966) directed towards her. In the second instance, the female grappled for approximately two to three seconds with male ED after he chased away male RY, one of the two males which was highly sexually preferred by the female (as measured by presentation frequency). In neither of these cases did the male attempt to mount the female prior to the grappling, and these were not considered instances of sexual coercion.

Male-Female Dominance Relations During the Pre-Breeding Season

Figure 6.6 shows the outcome of agonistic interactions between female TO and the four non-natal group resident males. During the pre-breeding period, the female never received aggression from any of the males nor experienced any agonistic losses, and was dominant to all males based upon consistent agonistic wins (Figure 6.6). Instances of grappling between this female and the resident males was also never observed during the pre-breeding season. Although there was no significant difference in

the number of agonistic interactions between this female and each of the males (Chi-square goodness of fit: $\chi^2 = 3.96$, df = 3, $p < 0.266$), male BR, the coercive male, showed the fewest instances of agonistic losses to the female during the pre-breeding season period.

DISCUSSION

Male Sexual Coercion in a Female Dominant Primate

This is the first documented case of male sexual coercion in *L. catta*. Sexual coercion is defined as the, "use by a male of force, or threat of force, that functions to increase the chances that a female will mate with him at a time when she is likely to be fertile, and to decrease the chances that she will mate with other males, at some cost to the female" (Smuts and Smuts, 1993). The event related here qualifies as sexual coercion in that 1) the male employed the use of force, 2) the male achieved the greatest number of mounts and greatest amount of time mounting this female as compared to all other males, despite the fact that he was the second-to-least preferred sexually among them (as measured by sexual presents), 3) the female was likely fertile, for *L. catta* females only mate when in estrus and conception is likely (Evans and Goy, 1968), and 4) the female appeared to experience curtailed mate choice as a result of the male's actions, as evidenced by shorter amount of time spent in mounts with two males to whom she showed the greatest sexual preference in the form of presents. Coupled with the observation that on at least one occasion the coercive male was able to gain penile intromission while the female unsuccessfully attempted to reject him, these data indicate

that male BR's sexually coercive tactics were successful in gaining him a disproportionately longer amount of time in copula with the female, and an overall greater number of mounts with the female as compared to other non-sexually coercive males in the group.

There is an ontogenetic link to female dominance in *L. catta*. Although female dominance begins to appear as early as 12 weeks in infants (Gould, 1990), unequivocal female dominance over males does not solidify until much later. Sauther (1993) noted that males were able to displace two-year-old nulliparous females, but were no longer able to do this following the females' first mating season. Among captive *L. catta* at the Duke University Primate Center, Pereira (1993c, 1995) found that female dominance over males gradually begins to emerge around puberty, which in captivity occurs at approximately 15 months of age. In the case reported here, though female TO 'won' all instances of female-male agonism during the pre-breeding season, the sexually coercive male was still able to be sexually forceful with her when she entered estrus during the mating season. One possibility is that this female was not yet fully socially dominant, as she was not successful at physically rejecting male BR's unwanted male sexual advances on her day of estrus. This evidence underscores the importance of ontogeny and maturity in the development of female social dominance.

The only similar instance of male aggression directed at a young female *L. catta* during the breeding season reported in the literature is an account by Sauther (1993) in which a male directed aggression towards a young nulliparous two-year-old female in Beza Mahafaly, Madagascar. A brief jump-fight ensued between the pair following a

mount attempt by the male. After the male and female cuffed one another during the jump-fight, the male reportedly jumped away (Sauther, 1993). Though this male briefly directed aggression towards this female during the breeding season, this event does not appear to be an instance of sexual coercion. It does, however, highlight the importance of age in the development of female social dominance.

Male Sexual Coercion: A Potential Consequence of Early Female Sexual Maturation

In many primates, greater food availability leads to female reproductive maturity at an earlier age (Japanese macaques, *Macaca fuscata*: Mori, 1979; Sugiyama and Ohsawa, 1982; Loy, 1988; Fukuda, 1988; Watanabe et al., 1992; Mori et al., 1997; rhesus macaques, *M. mulatta*: Schwartz et al., 1988; lion-tailed macaques, *M. silenus*: Lindburg and Harvey, 1996; baboons, *Papio cynocephalus*: Altmann et al., 1977, 1993; Strum and Western, 1982; Bercovitch and Strum, 1993; Altmann and Alberts, 2005). The same is true for *L. catta* females. Although females in the wild typically give birth for the first time at three years of age (Sussman, 1991), the provisioned *L. catta* females on St. Catherines Island can enter estrus as yearlings, and can give birth to their first infant at the age of two (Parga and Lessnau, 2005). This trend of early primiparity is also seen among *L. catta* in provisioned captive environments (DUPC: Taylor, 1986; Pereira, 1993c), and provisioned and/or resource-rich wild habitats (Berenty, Madagascar: Koyama et al., 2001).

Provisioned *L. catta* females can therefore enter estrus for the first time as yearling subadults before they become fully socially dominant over males, making them

vulnerable to male physical aggression and sexual coercion. Sauther (1991), Sauther and Sussman (1993), and Parga (2003) describe different mating strategies available to male *L. catta*. Now added to this list of strategies is the possibility for male sexual coercion of young sexually mature, but not socially dominant, females.

How Successful is Sexual Coercion as a Male Mating Strategy in *L. catta*?

The strategy of sexual coercion could have been employed by male BR in this study because he was not one of the more highly preferred mates of the group. The high dominance status of the sexually coercive male (who was ranked second in the group of four males) did not automatically make him highly sexually preferred. Two other same-aged resident males (RY and CH) had superior mating success; they were observed mounting a greater number of females during this mating season.

In any event, sexual coercion is only a strategy that is an option for *L. catta* males in provisioned or especially resource-rich wild areas, as those are the only locations in which non-socially dominant young females are likely to enter estrus due to early sexual maturation. Sexual coercion of very young and not yet socially dominant females is probably not a highly successful mating strategy for males, because these young females infrequently give birth to viable infants. Females two years of age have the lowest birth rates and infant survival rates of any age group on St. Catherines Island; less than 40% of females give birth at the age of two (Parga and Lessnau, 2005). In the wild, females within the youngest age groups (two to four years) likewise show low fecundity compared to older females (Berenty: Koyama et al., 2001; Beza Mahafaly: Sussman,

1991; Gould et al., 2003). Additionally, sexual coercion may entail a potential cost to the male. Coercive males may be the target of aggression from both the estrus females and her relatives (as evidenced by the aggression directed at the male in this study by the estrus female's mother). Sexual coercion as a male mating strategy may therefore be considered a last-resort for *L. catta* males not highly sexually preferred by females.

Nevertheless, a male may still opt to use force in attempting to mate with such a young socially non-dominant female, as this strategy may increase his reproductive success, even if only incrementally. The female who was the target of male sexual coercion in this study did not give birth to a viable infant the following birth season (though true conception, or lack thereof, is unknown). Therefore, this instance of sexual coercion against female TO by male BR did not increase his reproductive success. However, whether this male has ever attempted to utilize this coercive strategy with other young females is unknown. Future paternity analyses will determine how this male's reproductive success compares to that of other males in the St. Catherines Island *L. catta* population.

Is There Sexual Coercion in Other Female Dominant Prosimians?

In a select few other female dominant species, male aggression towards females during periods of mating have been reported. In Verreaux's sifaka (*Propithecus verreauxi*), a species considered female dominant (Richard and Heimbuch, 1975; Kubzdela, et al., 1992; Brockman, 1994), Brockman (1999) recounts one particular instance in which a male engaged in, "relentless sexual aggression," which involved both

clasp/mount attempts, and the male biting the female. This male sexual aggression was suggested to be a potential mating tactic of *P. verreauxi* males (Brockman, 1999). Similarly, in the mouse lemur (*Microcebus murinus*), although females are reported to be dominant to males (Radespiel and Zimmermann, 2001), Eberle and Kappeler (2004b) report instances of males "attacking" females while mate guarding them. Female submission and/or male aggression has also been noted during estrus in the black and white ruffed lemur (*Varecia variegata*) in both wild (Morland, 1993) and captive contexts (Shideler et al., 1983; White, pers. comm.), whereas outside of behavioral estrus females neither show submission to nor receive aggression from males (Morland, 1993). The blue-eyed black lemur (*Eulemur macaco flavifrons*), another reportedly female dominant species (Digby and Kahlenberg, 2002), also exhibits male aggression towards estrus females during mating in captivity and in the wild (Marsh, pers. comm.). Clearly, in several prosimians considered to be female dominant, the possibility for male sexual coercion exists, because male aggression towards females has been noted to occur in a mating context.

Female Mate Choice for "Persistent" Males?

Female aggression towards males which is discontinued (or only intermittently shown) during mating has been noted in other prosimian primates (*Varecia variegata*: Foerg, 1982; Shideler et al., 1983; Morland, 1993; *Propithecus verreauxi*: Brockman, 1994, 1999). This female aggression has been hypothesized to function as an invitation to mate, ensuring that strong males who can withstand the female's aggression copulate

(Foerg, 1982). Indeed, such male "persistence" in the face of female aggression/rejection may be evolutionarily adaptive for males, as in savanna baboons (*Papio cynocephalus*), where a male's number of ejaculations positively correlates with his mount attempts, and with the number of mount rejections he receives (Bercovitch, 1995).

It could be argued that the instance of sexual coercion reported in this paper may have functioned as female mate choice for a male showing persistence. However, the female in our study did not appear to sexually prefer the coercive male, but instead more highly preferred two other non-coercive males, as evidenced by her higher presentation rate to these other males. The fact that the majority of the coercive male's mounts were unsolicited by the female (Figure 6.2) strengthens this view. In addition, for the female to be eliciting the coercive male's persistence (e.g. Foerg, 1982), she should have directed just as much aggression toward him following solicited mounts as with unsolicited mounts, which was not the case (Figure 6.2). In sum, there is a strong possibility that the female's rejection of the coercive male was not mate choice for this male's persistence, but that instead, her mate choice was constrained by the activities of this coercive male.

CONCLUSIONS

In this study, a non-socially dominant yearling estrus female *L. catta* was the target of male sexual coercion by an unrelated resident adult male. This occurrence was likely a consequence of early reproductive maturity made possible by food provisioning. During the multiple copulatory mounts which comprised this instance of male sexual

coercion, the female was frequently unable to extricate herself from the male's forceful mount attempts, some of which were successful in that the male gained penile intromission. Several bouts of intense agonistic grappling between the pair ensued following repeated mount attempts by the male that were rejected by the female. Though the female did accept some of the male's mount attempts and even solicited copulation from him in the form of sexual presentation at times, the female more frequently presented to two other males who appeared to be more highly sexually preferred. Each of the more sexually preferred males in the group gained fewer overall mounts than the sexually coercive male, and each gained less time in copulatory mounts than did the sexually coercive male. These data therefore corroborate the evidence for an ontogenetic component to female social dominance in this species, and provide evidence for male sexual coercion in *L. catta*. Results suggest that via sexual coercion of young socially non-dominant estrus females, males can constrain female mate choice via sexual coercion, even in a female dominant primate.

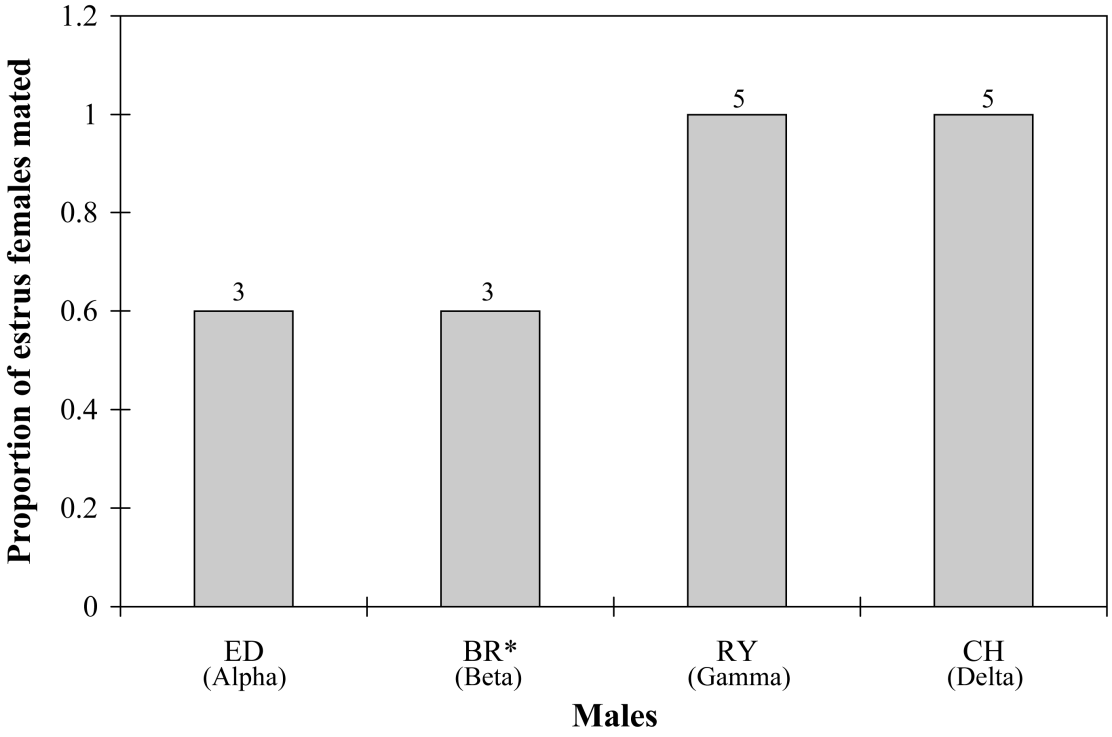

Figure 6.1: The proportion of estrus females in Group 2 during the 2002 mating season with which each male was observed to mate. Males are listed with their pre-breeding season dominance status. The sexually coercive male is denoted by an asterisk. Above each bar is the number of females mated. Mating data are from Table 5.1.

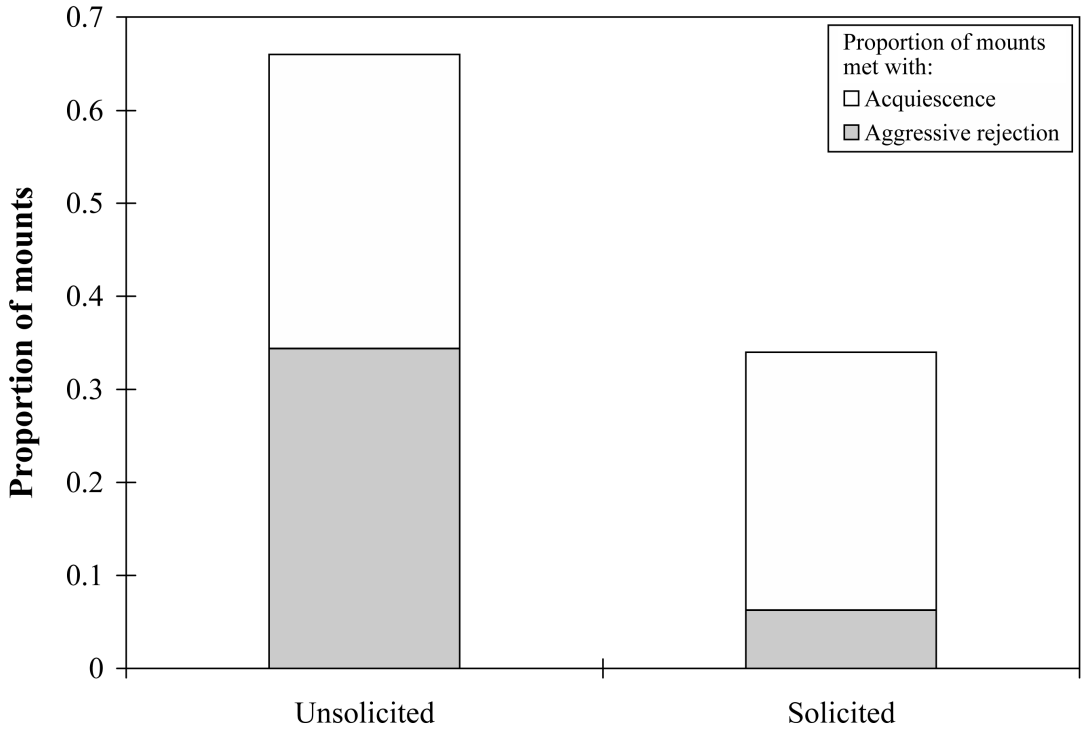

Figure 6.2: The proportion of mounts and mount attempts by the coercive male which were met with female aggressive rejection or sexual acquiescence by the female. Note that the majority of male mounts and mount attempts by this male (66%) were unsolicited by the female.

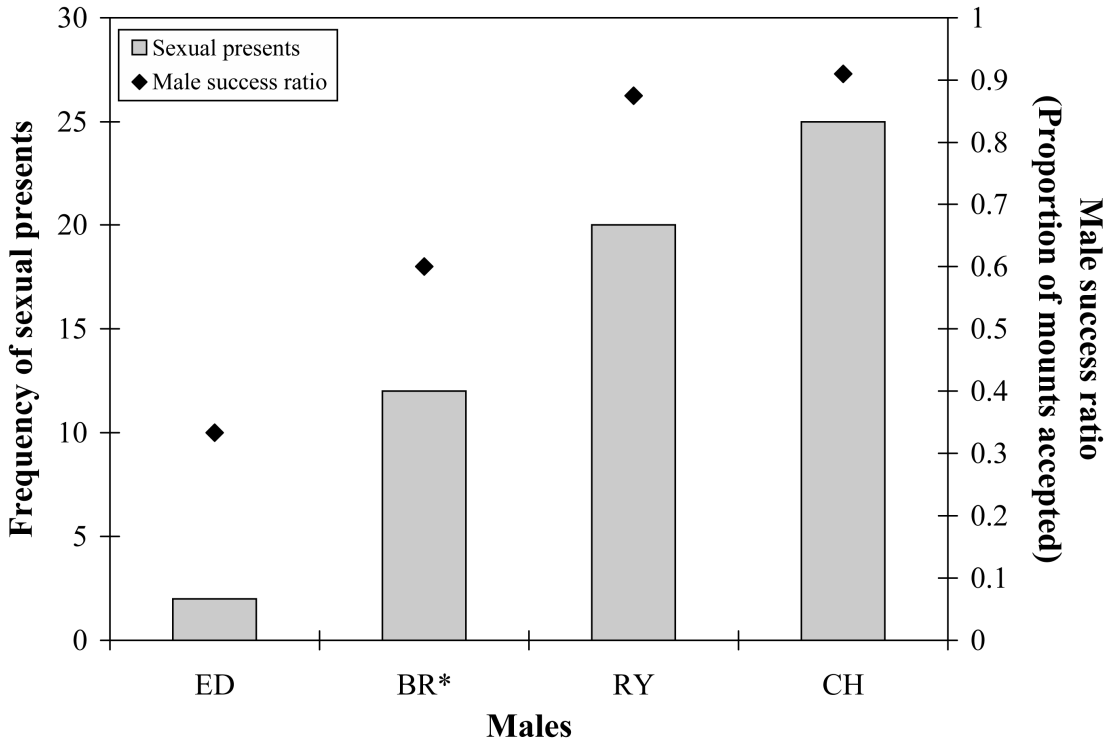

Figure 6.3: Frequency of female sexual presents and the success ratio of each male. There is a positive correlation between the number of sexual presents the estrus female directed towards each male, and each male's success ratio (Spearman rank correlation: $r_S = 1.0$, $n = 4$). Males are listed in order of descending dominance rank from left to right. Note that the sexually coercive male is one of the two least preferred males (as measured by sexual presents), and has one of the two lowest male success ratios. The sexually coercive male is denoted by an asterisk.

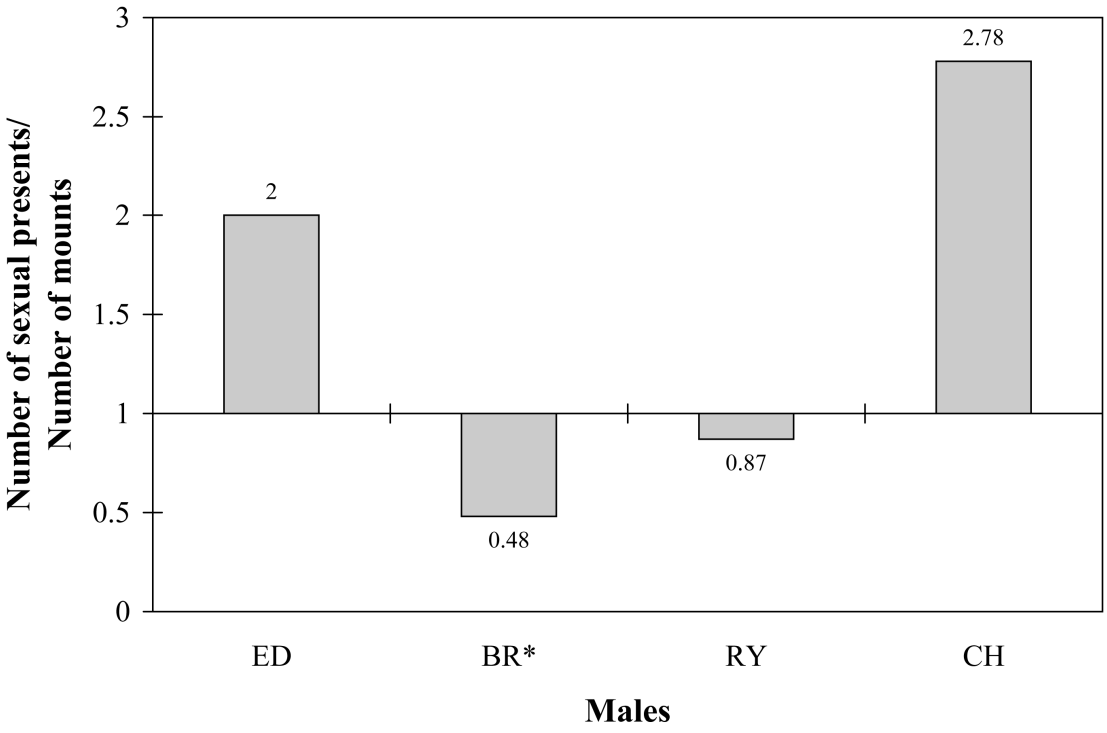

Figure 6.4: The ratio of female sexual presents relative to the number of mounts achieved by each male. Values above one indicate that the number of presents exceeded the number of mounts a male achieved. Values below one indicate that the number of mounts was greater than the number of presents a male received. The sexually coercive male, BR, achieved the lowest proportion of presents to mounts. Males are listed in order of descending dominance rank from left to right. The sexually coercive male is denoted by an asterisk.

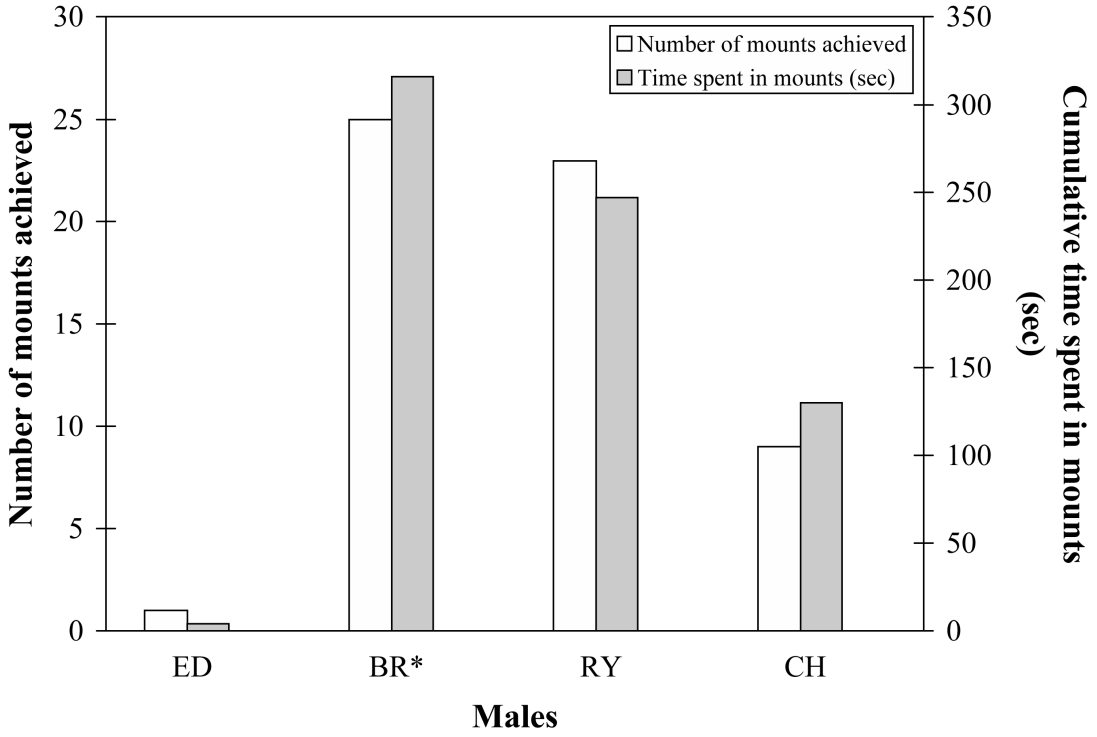

Figure 6.5: Number of mounts and the cumulative time spent in mounts by each male. The number of mounts by each male with female TO ($\chi^2 = 27.24$, df = 3, $p < 0.0001$) and the cumulative time spent in mounts with female TO ($\chi^2 = 323.26$, df = 3, $p < 0.0001$) differed significantly among males, and these two variables were positively correlated (Spearman rank correlation: $r_S = 1.0$, n = 4). The sexually coercive male achieved the greatest number of mounts with female TO and spent the longest cumulative time in mounts with this female. Males are listed in order of descending dominance rank from left to right. The sexually coercive male is denoted by an asterisk.

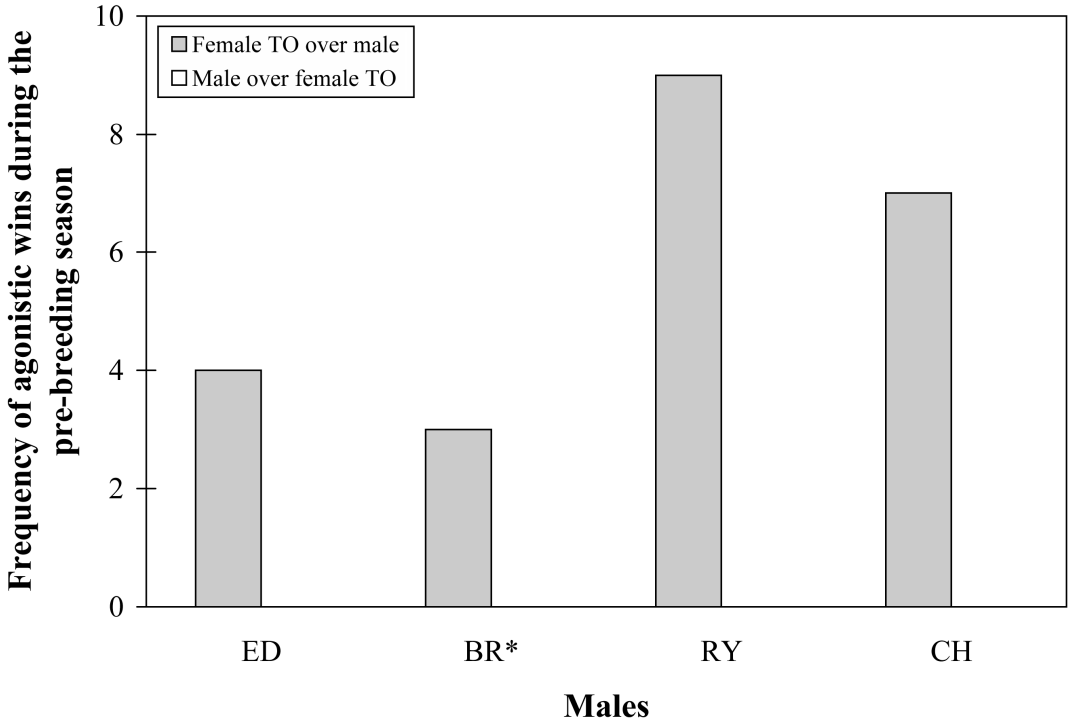

Figure 6.6: The frequency of agonistic wins by female TO over each male during the pre-breeding season. The frequency of female TO's wins did not significantly differ among males (Chi-square goodness of fit: $\chi^2 = 3.96$, df = 3, $p < 0.266$), although male BR showed the fewest agonistic losses to the female. There were no agonistic wins by any of the males over female TO. Males are listed in order of descending dominance rank from left to right. The sexually coercive male is denoted by an asterisk.

CHAPTER 7: SUMMARY AND CONCLUSIONS

Male Dominance Status and Mating Success

In group-living primates with male dominance hierarchies, high male dominance status is often associated with access to females, though there are many exceptions to this rule (Dewsbury, 1982). Though *L. catta* does not fit the priority of access model (Altmann, 1962), high-ranking males in this study were found to have some priority of access to females, though not *sole* monopolization potential (Chapter 2). Alpha males' priority of access was evidenced by their frequent presence as first mates, and even more strongly by their frequent ability to ejaculate first in the mating queue, which may confer a fertilization advantage (Chapter 2), as previously discussed by Sauther (1991) and Pereira and Weiss (1991).

Alternative Male Mating Strategies: Sneak and Evasive Copulations, and Rank Reversal

Although high-ranking *L. catta* males were often the first to mate with estrus females, they were by far not the only males to mate with females. In fact, many lower-ranking males garnered a fair degree of mating success due to alternative mating strategies (Chapter 2), including sneak copulations (copulating out of sight of the higher-ranking male or males), evasive copulations (copulations which were in full view of the higher-ranking male but in which the mating pair was far enough away from the male that he could not immediately interfere with copulation), and the rank reversal mating strategy (Chapter 3).

Disruptions of the male dominance hierarchy during the mating period had been previously described among *L. catta* males by a number of authors (Jolly, 1966, 1967; Budnitz and Dainis, 1975; Taylor, 1986; Koyama, 1988; Sauther, 1991; Pereira and Weiss, 1991; Gould, 1994, 1997; Pereira and Kappeler, 1997; Cavigelli and Pereira, 2000; Parga, 2002a, 2002b). However, this is the first work to describe the different forms that these dominance rank reversals take, and the first to provide quantitative data on the frequency of rank reversals during periods of female estrus. This is also the first study to identify the importance of two factors which appear to affect the occurrence and timing of rank reversals: 1) female sexual behavior (in the from of proceptive and receptive behavior) and 2) ejaculation.

Male dominance rank reversals in this study took three main forms (Chapter 3). "Type 1" rank reversals consisted of a single, clear shift in the relationship of two males which lasted for a period of minutes or hours, after which the male dominance ranks reverted to their pre-breeding season conditions. In contrast, "type 2" rank reversals were characterized by a high degree of variability in the outcome of successive agonistic interactions, with several dominance switches occurring throughout the rank reversal period. "Type 3" reversals consisted of a single agonistic win by a lower-ranking male, before and after which dominance relations resembled pre-breeding season conditions.

Males who reversed rank often did so following female sexual behavior directed towards them. A vast majority of males reversed rank only after they received proceptive or receptive behavior from the estrus female. Ejaculation also was an event which appeared to affect rank reversals. Most males who were observed to reverse rank

ejaculated before their rank reversal ended. Similarly, for higher-ranked males who ejaculated before losing rank (due to a lower-ranking male's reversal), rank loss typically closely followed their ejaculation. Male *L. catta* only ejaculate once with a female during a single estrus period (Sauther, 1991; Parga, 2003), so any further agonistic effort expended by males over access to an estrus female they already inseminated would only function as mate guarding, not as a mechanism to perform more ejaculations. Hence, female sexual behavior appears to stimulate lower-ranking males to perform rank reversals, and ejaculation seems to signal the impending loss of dominance for a male (Chapter 3).

Male Inter-Troop Transfer as a Mating Strategy

In addition to rank reversal, sneak copulations, evasive copulations, and attempting to attain high dominance rank prior to the beginning of the mating season, male *L. catta* inter-troop migration can be considered a male mating strategy. Male inter-troop transfer patterns on St. Catherines Island roughly approximate male transfer patterns in Madagascar (Jones, 1983; Sauther, 1991; Sussman, 1991, 1992; Gould, 1994) with respect to migration rates, duration of stay in a group, and the seasonality of male transfer (Chapter 4). The main difference in male transfer behavior between the two locations is earlier natal migration on St. Catherines, which is likely due to food provisioning causing the early sexual maturation of males.

Dominant males on St. Catherines Island transfer out of social groups more frequently than do lower-ranking males, which may indicate that higher-ranking males

can more easily endure the difficulty of inter-troop migration than lower-ranking males (Chapter 4). Transferring males were also significantly more likely to join a group with fewer males than the group from which they came, which suggests that males avoid those groups which would have higher levels of male-male competition during the mating season (Chapter 4).

Female Mate Choice

Although male-male competition is critically important for male mating success, female mate choice appears to have even greater importance to a male's mating success because of the presence of alternative male mating tactics, such as evasion or sneak copulations (Chapter 2). If using these alternative tactics successfully, a male can copulate to ejaculation without having to be successful in male-male physical combat. However, if a female overtly rejects the mating attempts of a male – even if he is highly successful at winning in male-male agonistic interactions – he is unlikely to have much mating success without female sexual acquiescence, given the female dominant nature of this species (Jolly, 1966, 1984; Budnitz and Dainis, 1975; Taylor, 1986; Kappeler, 1990a, 1993a; Pereira et al., 1990; Sauther, 1992; Nakamichi and Koyama, 1997; Pereira and Kappeler, 1997). It is for this reason that female mate choice is of primary importance to male mating success in *L. catta*. One notable exception to this rule is when extremely young females come into estrus before they fully achieve social dominance over males due to provisioning (see Chapter 6 for a case study of male sexual coercion in *L. catta*).

Females in this study were shown to sexually prefer novel males, though one of the most prevalent findings was that of extensive female multiple mating. Females mated with both high- and low-ranking males, and mated in many cases with the majority of males in their social groups, as evidenced by high selectivity index values (Chapter 5). Although other explanations for female multiple mating have been advanced (i.e. infanticide avoidance through paternity confusion: Hrdy, 1977, 1979, 2000; van Schaik et al., 1999, 2000), it is likely that female multiple mating functions as fertility assurance (Small, 1988) in *L. catta*, as has been previously suggested by Koyama (1988) and Sauther (1991).

A Comprehensive View of *L. catta* Male Mating Strategies

Sauther (1991) and Sauther and Sussman (1993) have provided a framework for the mating strategies used by *L. catta* males. As in the present study, Sauther (1991) found that higher-ranking males tended to mate first with females as they came into estrus, and notes the importance of male-male competition, mate guarding, and female choice. Male mating strategies listed in Sauther (1991) and Sauther and Sussman (1993) include pre-and post-copulatory mate guarding, mating with extra-troop females, the formation and removal of copulatory plugs, and inter-troop migration. Male mating strategies to be added to this list from the present study include sneak and evasive copulations (Chapter 2), male dominance rank reversals during periods of mating (Chapter 3), and male sexual coercion of young females, which is possible in provisioned or resource-rich areas where females may come into reproductive maturity without

attaining full social dominance over males (Chapter 6). Viewed together with previous studies (Jolly, 1966; Budnitz and Dainis, 1975; Taylor, 1986; Koyama, 1988; Pereira and Weiss, 1991; Sauther, 1991; Sussman, 1992; Sauther and Sussman, 1993; Gould, 1994, 1996), this project provides for a more comprehensive view of mating dynamics in *L. catta*.

Sexual Size Monomorphism in *Lemur catta*: Insights From This Study

The question still remains concerning the paradox of a species which shows physically aggressive male-male competition over females but also lacks sexual size dimorphism. The lack of sexual dimorphism in body size (Kappeler, 1990b) and dentition (Sauther et al., 2001) in *L. catta* when there is intense male-male physical contest competition over estrus females (Jolly, 1966; Taylor, 1986; Koyama, 1988; Pereira and Weiss, 1991; Sauther 1991; Gould, 1994; Gould et al., 2005; Parga, 2006) may be explained by selection for traits that enable a male to outperform other males in contest competition, not necessarily traits selecting for large male body size. As suggested by Kappeler (1990b, 1993b), perhaps traits involved in speed and agility are positively selected for, and more important in male fertilization success than large male body size. For example, in wild Verreaux's sifaka (*Propithecus verreauxi verreauxi*), reproductively successful males have been shown to be those with relatively long and muscular legs and intermediate body weight, which is thought to be important for locomotor behaviors rather than for overt fighting ability during male-male mating competition (Lawler et al., 2005).

Similarly, in *L. catta*, large male body size may not be as important as agility or stamina, for it was found in this study that younger males tended to receive sexual preference from a significantly greater number of estrus females (Chapter 4). This more frequent sexual preference directed towards younger males – rather than indicating female mate choice for young males – may indicate that younger males had the physical stamina to continually attempt to maintain proximity to estrus females despite frequent male-male competition.

The frequency of male rank reversals (Chapter 3) during periods of estrus and the success with which the rank reversal strategy gained mating opportunities for males (Chapter 2) is another line of evidence indicating that physically aggressive and *frequent* competition is important to male mating success during mating periods – both for males attempting to reverse rank, and for males attempting to maintain their rank throughout the estrus period. It is evident that physical stamina would be important during rank reversal periods for all males involved.

Sexual monomorphism in body size in *L. catta* may have also resulted from the importance of sperm competition (Parker, 1970) relative to other male morphological traits in determining male reproductive success. The widespread female multiple mating documented in this study (Chapter 5) indicates that there is likely intense sperm competition functioning in this species. If the raffle principle (i.e. the number of sperm each male ejaculates: Parker, 1990) controls male reproductive success in this species, then having large testes and high sperm counts (Short, 1979) may be more important to

male fertilization success than being physically large. This may be another reason for the sexual size monomorphism seen in this species.

Strier (1992) notes the conspicuous absence of male-male mating aggression among male muriquis (*Brachyteles arachnoides*), and has implicated sperm competition as a likely mechanism by which male intra-sexual competition occurs instead. Though *L. catta* compete intensely via agonism over reproductive females, sperm competition nevertheless appears to be important in *L. catta* mating (Sauther et al., 1999), as evidenced by the presence of copulatory plugs and their displacement (Sauther, 1991; Sauther and Sussman, 1993; Parga, 2003; Parga et al., 2006), and the relatively large testes sizes of *L. catta* males (Kappeler, 1997). Hence, if large male body size is not as important as sperm competition in determining male reproductive success in *L. catta*, this is one avenue by which sexual body size monomorphism may have evolved in this species.

Effects of Provisioning and Sex Ratio Differences Between SCI and Madagascar

Because this study was conducted at a novel location, it is important to summarize the effects of two variables that are likely responsible for the greatest deviations in mating behavior documented among *L. catta* on St. Catherines Island from the wild: 1) food availability on St. Catherines Island via provisioning, and 2) a female-biased sex ratio on St. Catherines Island as compared to Madagascar. One of the most notable effects of food provisioning on the reproduction of this species is the early age at mating for both males and females. Early sexual maturation means that males can mate for the

first time at 1 year of age (Chapter 2), as do females (Parga and Lessnau, 2005). This early sexual maturation appears to result in an earlier age at male migration (Chapter 3) than occurs in the wild.

One consequence of this earlier age at male migration might be that young males on St. Catherines Island have greater mating success at an earlier age than *L. catta* males in Madagascar. Another consequence of provisioning among primates pointed out by Smith (1993) is that more rapid weight gain in subadulthood may make males more likely to challenge older males for high dominance status. Hence, among non-provisioned *L. catta* in the wild, one prediction might be that rank reversals would not be performed by young (e.g. two- and three-year-old) males (as in this study: Chapter 3), but instead that the rank reversal strategy might only be found among prime-aged and older adult males. Early age at sexual maturation may also explain the statistically significant negative correlation between male age and female sexual preference in the form of proceptive and receptive behavior seen on St. Catherines. It is possible that young males in the wild may not experience the same levels of female sexual interest, as they become sexually mature at a much later age than do males on St. Catherines.

Finally, the unequal group sex ratios among *L. catta* on St. Catherines Island (Table 2.3) differs markedly from the typical 1:1 sex ratio found among *L. catta* groups in Madagascar (Jolly, 1966; Sussman, 1974, 1991; Budnitz and Dainis, 1975; Mertl-Milhollen et al., 1979; Jolly et al., 1982b). Because groups on St. Catherines have fewer males than groups in Madagascar, it may be easier for *L. catta* males on St. Catherines to monopolize estrus females, as there are fewer male competitors present. Accordingly,

high-ranking males on St. Catherines might sire a relatively greater number of offspring than high-ranking group males in the wild (i.e. there may be greater reproductive skew among *L. catta* on St. Catherines as opposed to *L. catta* in Madagascar).

Future Directions: Paternity Determination and the Strength of Comparative Studies

The completion of paternity analyses on St. Catherines Island *L. catta* will provide quantitative measures of male reproductive success for several individuals over a multi-year period. Using this information, the relative efficacy of different male mating strategies can be compared. An additional benefit is that many variables on St. Catherines Island (e.g. group sex ratios, food availability, female primiparous age, age at male natal dispersal) differ from wild *L. catta* populations in Madagascar in easily identifiable ways. Like many primates, *L. catta* exhibits a fair amount of behavioral plasticity (Sauther et al., 1999). Therefore, combining data from *L. catta* on St. Catherines Island with similar data collected on wild *L. catta* will allow patterns of reproduction to be studied under different environmental conditions, providing a more comprehensive view of different male reproductive strategies and their evolutionary significance.

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